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LES FACTEURS QUI INFLUENCENT L'UTILISATION DE TACTIQUE DE RECHERCHE ALIMENTAIRE CHEZ LE DIAMANT MANDARIN (*Taeniopygia guttata*)

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FACTORS AFFECTING SOCIAL FORAGING TACTIC USE IN THE ZEBRA FINCH (*Taeniopygia guttata*)

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FOREWORD

This doctoral thesis consists of four data chapters presented in the form of scientific articles. The first article (Chapter 2), "Increasing vulnerability to predation increases preference for the scrounger foraging tactic" is published in Behavioral Ecology (Volume 19, pages 131-138) and is co-authored by Kimberley Mathot and Luc-Alain Giraldeau. The second article (Chapter 3), "Testing dynamic variance-sensitive foraging using individual differences in basal metabolic rates of zebra finches" is published in Oikos (Volume 118, pages 545-552). This article is the outcome of a collaboration involving Kimberley Mathot, Sophie Godde, Vincent Careau, Don Thomas, and Luc-Alain Giraldeau. The third article (Chapter 4), "Family-related differences in social foraging: heritability of condition-dependent tactic use", has been submitted to Behavioral Ecology and Sociobiology. It is co-authored by Kimberley Mathot and Luc-Alain Giraldeau. The final article (Chapter 5), "Within-group relatedness can lead to higher levels of exploitation: a model and empirical test in socially foraging zebra finches (*Taeniopygia guttata*)", also co-authored by Kimberley Mathot and Luc-Alain Giraldeau. This manuscript has been provisionally accepted for publication in Behavioral Ecology.

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Although articles published or prepared for publication in scientific journals would normally each have a literature cited section, I have chosen to present a single bibliography at the end of the thesis in order to economise paper.

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RÉSUMÉ

Lorsque des animaux recherchent de la nourriture en groupe, les individus peuvent investir dans la quête de nourriture (tactique producteur) ou dans la recherche d'occasions d'exploiter les découvertes alimentaires d'autres membres du groupe (tactique chapardeur). Les deux tactiques sont maintenues dans les groupes selon la fréquence-dépendance, et des modèles théoriques prédisant une proportion stable des tactiques utilisées à l'échelle du groupe ont été développés. Cependant, on sait peu de chose au sujet des facteurs qui influencent les décisions individuelles d'investissement dans la tactique producteur ou chapardeur. En utilisant des diamants mandarins (*Taeniopygia guttata*) comme système modèle, je teste deux variables d'état qui peuvent influencer la prise de décision relative à une tactique. Chez les oiseaux qui se nourrissent au sol, les individus sautillent en gardant la tête dressée lorsqu'ils font du chapardage et occupent des positions au centre de la volée ; ce sont deux comportements qui accroissent leurs chances d'échapper à des prédateurs. J'ai donc prédit qu'accroître la vulnérabilité à la prédation d'un individu favoriserait une plus grande utilisation de la tactique chapardeur. Conformément à cette prédiction, les individus ont accru leur utilisation de cette tactique au cours des expériences augmentant leur vulnérabilité à la prédation (la taille des plumes du vol, ou rémiges, pour réduire la capacité à s'envoler pour échapper à un prédateur). En me fondant sur des prédictions de la théorie de l'approvisionnement sensible à la variance, j'ai aussi testé si les variations individuelles du métabolisme basal sont associées à des usages différents des tactiques sociales de quête de nourriture. J'ai supposé que les individus possédant un métabolisme basal élevé avaient plus de chances d'avoir un déficit énergétique, donc utiliseraient plus la tactique alimentaire aux résultats moins variés, le chapardage. J'ai effectué des tests avec des données appareillées d'individus ayant un métabolisme basal élevé ou bas dans la même volée. J'ai trouvé que les individus ayant un métabolisme basal élevé utilisaient davantage la tactique chapardeur que les individus au métabolisme bas. Différents aspects de l'état de l'individu sont héritables, y compris le métabolisme basal. Conséquemment, le fait que le choix d'une tactique soit influencé par l'état de l'individu suggère que l'usage d'une tactique est peut-être aussi héritable. Nous avons vérifié si l'usage d'une tactique alimentaire est héritable en comparant les tactiques utilisées par des frères et des sœurs testés dans des volées différentes. Nous avons trouvé que le choix de la tactique est similaire pour des individus apparentés. Ces résultats indiquent que l'utilisation d'une tactique par les individus n'est pas entièrement flexible, et pourrait influencer les décisions relatives à la formation des groupes chez les animaux qui s'approvisionnent socialement. Enfin, j'ai développé un modèle qui prolonge le modèle classique producteur-chapardeur (qui maximise le taux de consommation) de sorte à tenir compte des effets de l'aptitude phénotypique inclusive dans le cas de l'approvisionnement par des groupes d'individus apparentés. Le modèle prend en considération les conséquences de l'aptitude phénotypique inclusive de la production de nourriture et du chapardage au moment de rechercher de la nourriture avec des individus apparentés. Il permet aussi aux individus de faire preuve de différents niveaux de tolérance selon que le chapardage est effectué par des individus apparentés ou non. Le modèle prédit

qu'un fort degré d'apparentement peut aboutir à de plus grands niveaux d'exploitation lorsque les producteurs permettent le chapardage par des individus apparentés, mais imposent des coûts aux chapardeurs non apparentés (ceux-ci sont, par exemple, la cible de comportements agressifs). Nous avons testé cette prédiction chez des diamants mandarins captifs qui s'approvisionnent soit en volées de frères et sœurs, soit en volées d'individus non apparentés. Nous avons trouvé que les volées d'oiseaux apparentés comprenaient de plus grandes proportions de chapardage et des niveaux plus bas d'interactions agressives, comparativement aux volées d'oiseaux non apparentés. Ces résultats indiquent que, sous l'effet de la pression de la sélection de parentèle, les producteurs permettent à des individus apparentés de chaparder. Étonnamment, bien que des niveaux de chapardage plus élevés soient généralement associés à une baisse du taux de découverte de parcelles de nourriture, les groupes d'individus apparentés n'ont pas connu une réduction du taux de découverte de parcelles alimentaires, comparativement aux groupes d'individus non apparentés. Cela s'explique probablement par le fait que moins de temps a été consacré à des interactions agressives au sein des groupes d'individus apparentés. Étant donné que les groupes d'individus apparentés ont des taux de découverte des parcelles alimentaires équivalents à ceux des groupes formés d'individus non apparentés, tout en ayant moins d'interactions agressives, il est nettement bénéfique de se regrouper avec des individus apparentés, même quand ces groupes ont de plus grandes proportions de comportements d'exploitation. Le résultat de cette expérience souligne l'importance de tenir compte des individus – producteurs ou chapardeurs – qui contrôlent la fréquence de l'exploitation, étant donné que l'observation d'une exploitation accrue entre individus apparentés ne peut être comprise qu'à la lumière de changements de la propension à chaparder ainsi que de la propension à tolérer le chapardage en fonction de la parenté.

Mots clés: approvisionnement social, tactiques alternatives, variation individuelle, condition dépendance, sélection de parentèle

ABSTRACT

When animals forage in groups, individuals can invest in searching for food (producer tactic), or in searching for opportunities to exploit the food discoveries of group mates (scrounger tactic). Both tactics are maintained in groups via frequency dependence, and theoretical models have been developed which predict the stable frequency of tactics at the level of the group. However, relatively little is known about the factors that influence individual investment decisions in producer-scrounger alternatives. I tested two state-variables which may influence tactic use decisions using the zebra finch (*Taeniopygia guttata*) as a model system. In ground feeding birds, individuals hop with the head up when engaged in scrounger and occupy central positions in the flock, both of which may provide greater anti-predator benefits. Therefore, I predicted that increasing an individual's vulnerability to predation would favour higher use of the scrounger tactic. Consistent with the prediction, individuals increased their use of the scrounger tactic following experimental increases in their vulnerability to predation (using flight feather clippings to reduce predator escape flight performance). I also tested whether individual variation in basal metabolic rate (BMR) is associated with differences in the use of social foraging tactics based on predictions from variance-sensitive foraging theory. I assumed that individuals with a higher BMR would have a higher probability of energetic shortfall and consequently have a higher use of the foraging tactic that yields less variable rewards, scrounger. I conducted paired tests of high and low BMR individuals in the same flocks and found that high BMR individuals had a higher use of scrounger than their low BMR counterparts. Many aspects of individual state are heritable, including BMR. Consequently, the finding that tactic use decisions are influenced by individual state suggests the possibility that tactic use may also be heritable. We tested for heritability of tactic use by comparing the tactic use of full-siblings tested in different flocks, and found that there were strong family-related differences in tactic use. This finding suggests that the tactic use of individuals is not entirely flexible, and has important implications for group formation decisions in social foragers. Finally, I developed a model which extended the classic rate-maximizing producer-scrounger model in order to incorporate the inclusive fitness effects when foraging in groups of kin. The model takes into account the inclusive fitness consequences of 'producing' (searching for food) and 'scrounging' (exploiting the food discoveries of others) when foraging with relatives, while simultaneously allowing individuals to show differential tolerance towards scrounging by kin versus non-kin. The model predicts that increased relatedness can lead to higher levels of exploitation when producers are kin-selected to allow scrounging from relatives but impose costs on unrelated scroungers, for example by being aggressive towards them. We tested this prediction empirically in captive zebra finches foraging either in flocks with full-siblings or in flocks of unrelated individuals. Flocks of related zebra finches had higher frequencies of scrounging and lower levels of aggressive interactions compared with flocks of unrelated zebra finches. The results suggest that producers may be kin-selected to allow relatives to scrounge. Surprisingly, although increased levels of scrounging are typically associated with a decrease in food patch discovery rate, groups of related individuals did not suffer any

reduction in patch discovery rates compared with non-kin groups. This presumably arose because less time was spent in aggressive interactions in kin groups. Given that kin groups have patch discovery rates equal to those of non-kin groups while at the same time experiencing lower levels of aggressive interactions, there is a net benefit to grouping with kin, even when kin groups exhibit a higher frequency of exploitative behaviours. This result highlights the importance of considering which individuals control the frequency of exploitation – scroungers or producers - as the finding of increased exploitation among relatives can only be understood in light of the combined changes in propensity to scrounge and the propensity to tolerate scrounging as a function of mean relatedness.

Key words: social foraging, alternative tactics, individual variation, condition-dependent, kin-selection

CHAPTER 1
GENERAL INTRODUCTION

This introduction is divided into 5 sections. Section 1 begins with a general discussion of alternative tactics. Examples of alternative tactics are provided followed by a discussion of the factors that allow alternative tactics to be maintained within populations. Section 2 deals more explicitly with a specific example of alternative tactic use, producer-scrounger games. The characteristics of producer-scrounger games are described, and examples from a range of contexts are provided. Section 3 gives a broad overview of producer-scrounger games in a social foraging context. This is the producer-scrounger framework considered in each of the following chapters. The specific objectives of the thesis are also outlined. In Section 4, I provide general information on the study species used for all experiments, the zebra finch (*Taeniopygia guttata*), emphasizing the traits that make it particularly amenable for use as a model species. Finally, in Section 5, I provide a brief thesis overview, highlighting the main objectives of each of the following chapters.

1.1 Alternative tactics

The optimality approach has been widely applied in ecological studies to understand the distribution of phenotypic and behavioural traits within populations. The fundamental assumption of the optimality approach is that the trait that is 'best' for an individual's reproduction and survival will prevail after natural selection (Dawkins 1980). However, numerous examples exist where multiple forms of a trait are maintained in a population, often to the detriment of individual fitness. In order to understand how this can occur, consideration of additional factors, such as frequency and condition dependence, is needed (Brockmann 2001).

1.1.1 Frequency dependence

Frequency dependence exists when the fitness value of a given trait is a function of its relative occurrence in the population. The classic example used to explain frequency dependence is the hawk-dove game. The following example is adapted from Maynard Smith (1982). Imagine a population consisting two types of individuals: hawks and doves. Hawks fight aggressively over resources when they encounter another individual, until a winner is determined. When a hawk encounters a hawk, the winner obtains the full value of the resource (V), and the loser suffers injury (I). On the other hand, doves split the resource equally when they encounter other doves, and lose the resource without incurring injury when they encounter hawks (because they immediately accept defeat).

In a population comprised almost exclusively of hawks, hawks will obtain the full resource value (V) in half of all encounters, and suffer the cost of injury (I) in half of all encounters, resulting in an average payoff of (V-I)/2. Doves will receive an average payoff of zero. As the frequency of doves increases in the population, hawks do progressively better because they will pay the cost of losing an agonistic encounter less frequently. When the population is comprised almost exclusively of doves, the mean payoff of hawks will approach V, while the mean payoff of dove will be V/2.

Figure 1.1 illustrates the frequency dependence of hawk and dove tactics. The exact slopes of the fitness lines for hawk and dove will vary depending on the value of the resource and the cost of injury. However, the key points to note are the following: 1. each tactic does better relative to the other tactic when it is rare. This will tend to maintain both tactics in a population because in a population that drifts towards a low proportion of dove, doves will have an advantage over hawks and will increase in frequency in the next generation. Conversely, in a population that happens to drift towards a high proportion of doves, hawks will have an advantage over doves and the frequency of doves will tend to decrease in the next generation, 2. The stable proportion of hawks and doves in a population occurs where the mean fitness of hawks is equal to the mean fitness of doves. This proportion is referred to as an evolutionarily stable strategy (ESS), because if the population ever drifts from this

proportion, natural selection will tend to restore it to the ESS, and 3. Individual fitness is not maximized at the ESS. All individuals would do better if the population consisted exclusively of doves.

The hawk-dove game is a theoretical example that illustrates how frequency dependence can operate to maintain multiple values of a trait in a population. Stability is the optimization criterion used to determine the frequency of traits in a population, as opposed to fitness or a surrogate of fitness as is typically used in the optimality approach. Frequency dependence appears to be an important mechanism maintaining alternative tactics in many systems (see Brockmann 2001 for review).

1.1.2 Condition dependence

Another means through which multiple values of a trait can be maintained in a population is if the fitness value of alternative tactics varies as a function of condition. For example, it may not be beneficial to engage in costly aggression over a resource if resources are abundant and an alternative resource can easily be located. Then, the strategy played by individuals may be: if resources are rare, fight for them, otherwise, avoid confrontations. This is an example of a strategy that is conditional on environment (Davies 1982) and would result in multiple tactics being maintained in the population. Alternatively, the cost of fighting may vary as a function of body size, such as if larger individuals are more likely to win contests. The strategy might then be phrased as: fight for the resource if you are big, otherwise do not fight. This is an example of a strategy that is conditional on phenotype (Davies 1982).

In many cases, alternative reproductive tactics result from a condition-dependent strategy (Gross 1996 and references therein). For example, if females prefer larger males, then the payoff for displaying males will increase with increasing body size. In contrast, the payoff for males that sneak copulations may be independent of body size, or even decrease with increasing body size, if smaller males are better at approaching females undetected. This type of conditional-strategy is shown in Figure 1.2. There are many other examples of behavioural strategies that are conditional on phenotype. Habitat selection (Ydenberg et al.

2002), anti-predator behaviours (Wasson and Lyon 2005), mating tactics (Pearcy et al. 2005), and parental care (Badyaev and Hill 2002; Winkler and Allen 1995) decisions can all be influenced by the condition or phenotype of the individual. The key feature of condition-dependent strategies is that fitness will not be equalized across tactics and individuals employing the tactic that provides the lower fitness payoff are often referred to as "making the best of a bad job".

1.1.3 Condition dependence with frequency dependence

While the literature has largely treated condition dependence and frequency dependence as two alternative means of maintaining multiple traits in a population, both mechanisms can operate simultaneously (Brockmann 2001). Some theoretical work has been done to determine the ESS solutions for cases where alternative tactics depend on both environmental conditions and the frequency of those tactics in a population, for example, the stable frequency of producer and scrounger foraging tactics under different food distributions (Vickery et al. 1991). However, notably less theoretical research has gone into finding the ESS solutions for alternative tactics that are dependent on both frequency and phenotype (Repka and Gross 1995 , but see Barta, 1998).

Maintenance of multiple traits in a population via both frequency and phenotype dependence versus frequency dependence alone has important implications. When frequency dependence alone underlies tactic use, the fitness value of each tactic will be equal (on average) and individual differences in fitness will not be correlated with differences in tactic use (Dawkins 1980). In contrast, when tactic use is dependent on both phenotype and frequency, the fitness value of each tactic will be equal on average within, but not between, phenotypes, and fitness differences among individuals may be related to differences in tactic use (Parker 1982; Repka and Gross 1995). Predicting the stable mixture of tactics in a population becomes more complex in this scenario, because the tactic(s) adopted by any given individual will depend both on its own phenotype and the frequency of the alternative tactics being played by other group members, which itself is influenced in part by their own phenotypes (Repka and Gross 1995).

Many systems are likely to exist where both phenotype and frequency will influence tactic use decisions (Repka and Gross 1995), including producer and scrounger tactic use in social foragers. Because producer-scrounger games are amenable to study in the laboratory, where manipulations of both tactic frequency (Flynn and Giraldeau 2001; Mottley and Giraldeau 2000) and phenotype are possible, they present a viable system for studying the combined influence of frequency and phenotype on tactic use decisions.

1.2 Producer-scrounger games: A general overview

Producer-scrounger relationships exist wherever alternative tactics can be classified as investing in resource (producer tactic), and exploiting the investment of another (scrounger tactic) (Barnard 1984). The investment in a resource can take various forms, including investment of time or energy (Barnard 1984). 'Producer' individuals would do better if their investment in a resource were not exploited by 'scrounger' individuals, but the presence of scroungers is inevitable whenever there is a benefit from not having to invest in the production or discovery of the resource in question (Barnard and Sibly 1981; Giraldeau and Caraco 2000). The extent of this benefit will depend on how costly it is to invest in a resource, how many 'producers' there are from whom to scrounge, the cost of scrounging in terms of defence or retaliation by 'producers', and the value of the resource (Barnard 1984).

Examples of producer-scrounger relationships are widespread. In bacteria, some individuals produce siderophores, extra-cellular molecules which aid in the uptake of iron, which is critical for growth and survival (Ratledge and Dover 2000). Siderophores are released extracellularly and are metabolically costly to produce (West and Buckling 2003). Other bacterial strains do not invest in siderophore production, but utilize the siderophores produced by others (West and Buckling 2003). Another example of producer-scrounger relationships in unicellular organisms comes from fruiting body formation in bacteria and amoebas. In bacteria and amoebas, some individuals will invest in forming the stalk structure, while others will exploit this investment to benefit their own dispersal as fruiting bodies (Buss 1982; Fiegna and Velicer 2005; Hudson et al. 2002).

Many alternative reproductive tactics can also be viewed in a producer-scrounger framework. In ruffs (*Philomachus pugnax*) some males invest time and energy displaying at leks to attract females, while others males (satellites) will sneak copulations with females that have been attracted to the leks (Hogan-Warburg 1966; van Rhijn 1973). Similarly in many species of frogs, some males will call to attract females, putting themselves at increased risk of predation, while other males will intercept females as they approach calling males, thereby avoiding the cost of increased predation risk (Lucas et al. 1996). Brood parasitism, which is particularly common in waterfowl, is another major class of reproductive tactics that can be effectively categorized into producer and scrounger roles (Barnard 1984). In many species of birds, females will lay their eggs in the nest of another female, exploiting the incubation and provisioning efforts of the nest attending female (Andersson 1984).

Arguably the best-studied example of the use of producer-scrounger tactics comes from the field of social foraging (Giraldeau and Caraco 2000). When animals forage in groups, individuals can invest in searching for food (producer tactic), or in searching for opportunities to exploit the food discoveries of congeners (scrounger tactic) (Giraldeau and Caraco 2000). Producer-scrounger foraging is the framework used throughout this thesis for investigating phenotype-dependent tactic use in a frequency-dependent game.

1.3 Producer-scrounger games: Social foraging

One of the critical features of producer-scrounger foraging is that the alternative tactics are mutually exclusive (Giraldeau and Beauchamp 1999; Giraldeau and Caraco 2000). Although individuals can alternate between both tactics, the two tactics cannot be performed simultaneously (Giraldeau and Caraco 2000). Producer-scrounger tactics are maintained in groups via frequency-dependence: each tactic does better relative to the other tactic when it is rare (Figure 1.3). Consequently, at some intermediate frequency of tactic use, both tactics receive equal payoffs (Giraldeau and Caraco 2000; Mottley and Giraldeau 2000). This point is known as the stable equilibrium frequency (SEF) and is analogous to an evolutionarily stable strategy, ESS (Mottley and Giraldeau 2000). Natural selection is the mechanism which

leads populations towards an ESS, while a SEF does not imply any mechanism (Giraldeau and Dubois 2008). When the SEF is attained via behavioural adjustments, it is also known as a behaviourally stable solution, or BSS (Giraldeau and Dubois 2008).

1.3.1 Group-level tactic use

The SEF of tactic use is influenced by several factors, including group size, food distribution, and energetic state. The SEF of scrounger is predicted to increase with increasing group size (Vickery et al. 1991), a prediction which has been confirmed empirically in nutmeg mannikins (*Lunchura punctulata*) (Coolen 2002). The predicted effect of food distribution on the SEF of scrounger tactic is less straight-forward, with different predictions being generated by rate-maximizing (Vickery et al. 1991) and variance-sensitive (Caraco and Giraldeau 1991) models. Rate maximization models predict that as the fraction of a food patch that can be monopolized by the finder before the arrival of joiners (ie. the finder's share) increases, so should the relative use of producer tactic in a group (Vickery et al. 1991). This is because each finding event yields a relatively greater payoff than each joining event as the finder's share increases. The spatial distribution of food influences the finder's share such that a few seeds dispersed among several patches will result in a higher finder's share compared with a seed distribution where there are many seeds clumped into a few rich patches (Livoreil and Giraldeau 1997). Empirical support for rate-maximizing social foraging tactic choice has been found in nutmeg mannikins (Coolen et al. 2001).

While rate-maximizing producer-scrounger models predict no effect of food patch density on the SEF of tactic use, variance-sensitive producer-scrounger models predict that as the density of food patches increases, so should the relative use of the scrounger tactic (Caraco and Giraldeau 1991). This prediction comes about because as the density of food patches increases, so too does the mean intake rate of group members. Consequently, because of their good energetic condition, individuals should avoid variance and increase their relative use of scrounging, the foraging tactic that has lower uncertainty in mean return (Koops and Giraldeau 1996; Lendvai et al. 2004; Wu and Giraldeau 2004), as their likelihood of energetic shortfall is reduced. Empirical support for this predicted effect of food

distribution on the SEF of scrounger tactic use has been documented in starlings (*Sturnus vulgaris*) (Koops and Giraldeau 1996).

In variance-sensitive producer-scrounger models, the predicted effect of the food patch density comes about via the effect that overall food abundance has on the energetic state of individuals. Thus, energetic state itself influences the SEF of tactic use. When individuals are in poor condition and face a comparatively high probability of starvation, they should be risk-prone, as this will maximize their probability of survival (Stephens and Krebs 1986). In social foraging groups, this means that increasing the probability of starvation of group members should result in an increase in the SEF of producer. Studies manipulating the probability of energetic shortfall in flocks of nutmeg mannikins support this prediction (Wu and Giraldeau 2004).

However, variance-sensitive foraging decisions can also be considered in light of the time remaining in a foraging bout. An animal low on reserves but with many hours available to achieve its required intake is in a very different situation than an animal low on reserves with only moments available to achieve it required intake (McNamara and Houston 1996). Dynamic variance sensitive foraging models predict that early in the foraging bout, low energy reserves should favour variance-averse behaviour (scrounger tactic), while the same energetic state late in the foraging bout should favour variance-prone behaviour (producer tactic) (Barta and Giraldeau 2000). Based on changes in the frequency of individuals in good versus poor energetic state throughout the day at the level of the group, the predicted use of scrounger is expected to be highest early in the day, decline in the middle, and increase again towards the end of the foraging period (Barta and Giraldeau 2000). The predictions of daily patterns of scrounger use have yet to be tested empirically.

Predation risk has also been considered as a factor influencing producer-scrounger foraging decisions. Differences in head orientation associated with producer and scrounger tactics may influence the inherent vigilance of individuals employing these two tactics. In ground feeding birds, the head is predominantly orientated downwards to locate food when producing, whereas scrounging requires the head to be in a more elevated position to observe

which congeners have successfully located food (Coolen et al. 2001). Several studies have demonstrated that individuals that use foraging behaviours with a head-up orientation have greater inherent vigilance compared with those that use more head-down foraging behaviours (Barbosa 1995; Elgar et al. 1986; FitzGibbon 1989; Lima and Bednekoff 1999). This implies that the scrounger tactic may provide individuals with a greater inherent level of vigilance and the prediction that follows from this is that groups foraging under increased levels of predation risk should show higher relative use of scrounger foraging tactics compared with groups feeding under relatively low levels of predation risk.

While theoretical work has predicted an effect of predation risk on the SEF of scrounging (Barta and Giraldeau 2000), empirical studies testing this prediction have yielded contradictory results. In northwestern crows (*Corvus caurinus*), the presence of predators had no effect on scrounger tactic use (Ha and Ha 2003). Similarly, in flocks of nutmeg mannikins, experimentally increasing the perceived risk of predation by increasing the distance between the foraging site and protective cover had no effect on the relative use of scrounging tactic (Coolen and Giraldeau 2003). Consequently, Coolen and Giraldeau (2003) concluded that scrounging and anti-predator vigilance are incompatible, at least under conditions similar to those used in their study. In contrast, studies in free ranging ravens (*Corvus corax*) (Bugnyar and Kotrschal 2002), and tree sparrows (*Passer montanus*) (Barta et al. 2004), reported higher use of scrounger tactics in groups foraging under increased predation risk, although in both cases, mechanisms other than compatibility of scrounging and vigilance behaviours may account for the shift.

Another factor which may influence the group level SEF of scrounger is relatedness. Although no formal theoretical framework has been developed to address this, the potential for relatedness to influence the SEF of scrounger has been acknowledged previously (Vickery et al. 1991). From the point of view of a scrounger, scrounging food from a relative will have a negative effect on inclusive fitness while scrounging from a non-relative will not. Thus, relatedness may be expected to favour a reduction in the frequency of scrounging, which would be consistent with the general view that grouping with kin provides a means of mitigating the costs of exploitation by group members (Eckman et al. 2004; Frank 2003;

Hamilton 1964). In contrast, from the point of view of a 'producer', allowing kin to exploit them is less costly than allowing non-kin to exploit them. Therefore, producers may be expected to allow joining by kin, but aggressively defend patches against non-kin joiners. In this case, kin selection may lead to higher levels of the exploitative foraging tactic.

1.3.2 Individual tactic use

Initial work on producer-scrounger foraging focused mainly on factors that influence the group level SEF of producer-scrounger alternatives. Comparatively few studies have attempted to address how individuals within the group contribute to reaching the SEF. A group level SEF of 30% scrounger can be reached in various ways. All individuals could invest 30% of their search effort in the scrounger tactic and 70% of their effort in the producer tactic. Alternatively, 30% of individuals could invest all their search effort as scroungers, and the remaining 70% of individuals could invest all their search effort as producers. However, it is also possible that all individuals have different investment levels, so long as the group level investment equals the SEF. In fact, this latter scenario appears to be the most common, with several studies reporting that the SEF of scrounger tactic use is achieved through differing levels of investment in the scrounger tactic among group members (Barta et al. 2004; Beauchamp 2001; Bugnyar and Kotrschal 2002; Ha and Ha 2003).

One suggestion for individual differences in the use of producer-scrounger alternatives is that such differences are random and arbitrary (Thibaudeau 2004). Random and arbitrary differences in individual allocation to producer and scrounger tactics could arise due to the frequency dependence of payoffs between the two tactics. When producers are rare, they do relatively better than scroungers and vice versa (Giraldeau and Caraco 2000; Mottley and Giraldeau 2000). Consequently, the best strategy for each individual depends on what others in the group happen to have ended up doing. Even if individuals do not differ in their ability to use producer and scrounger tactics, by chance, some individuals in a group will discover food patches sooner than others, opening the door for scrounging by other group members. As such, differences in the relative use of producer and scrounger tactic that arise in a group may be random and arbitrary.

However, several studies have noted that individual differences in tactic use are consistent even when the SEF of the group changes. When the distribution of food patches becomes more clumped, such that a higher SEF of scrounger is predicted, nutmeg mannikins that had the highest use of scrounger in the initial condition relative to their group mates tended to have the highest use of scrounger under the new conditions (Thibaudeau 2004). Similar results were found for wild Carib grackles (*Quiscalis lugubris*) (Morand-Ferron et al. 2007). Individual consistency in tactic use has also been recorded under changing flock compositions in both zebra finches (Beauchamp 2001), and starling (Koops and Giraldeau 1996). These results all suggest that there may be intrinsic differences between individuals in their tendency to use alternative tactics. However, relatively little is known about which factors may be influencing inter-individual differences in tactic use (Beauchamp 2000a; Beauchamp 2001; Thibaudeau 2004).

One factor that has been considered explicitly in terms of its effect on individual differences in tactic use is dominance (Barta and Giraldeau 1998; Giraldeau et al. 1990; Liker and Barta 2002; Thibaudeau 2004). Theoretical analyses suggest dominant individuals should have a higher use of the scrounger tactic, while subordinates should have a higher use of producer (Barta and Giraldeau 1998). This prediction comes about because if dominant individuals are competitively superior to subordinates, then they will be able to displace subordinates from patches that they join, consequently enjoying a higher payoff from the scrounger tactic compared with subordinates. Some studies have found support for this prediction. In house sparrows (*Passer domesticus*), individuals of higher dominance rank have a higher use of the scrounger tactic compared with subordinates (Lendvai et al. 2006; Liker and Barta 2002). This result was also found in nutmeg mannikins, but only for females (Thibaudeau 2004). In Mexican scrub-jays (*Aphelocoma ultramarina*) individuals preferentially join individuals of lower dominance rank (McCormack et al. 2007). However, dominance is not related to tactic use in the zebra finch (Beauchamp 2006; Giraldeau et al. 1990). Species-related differences in the extent of dominance asymmetries between individuals may be an important determinant of whether individual tactic use decisions are influenced by dominance (Barta and Giraldeau 1998).

There is also evidence that early experience may shape individual producer-scrounger foraging preferences (Katsnelson et al. 2008). In one study, juvenile hand-reared house sparrows were imprinted on a stuffed model of a female house sparrow which either led them to patches containing food (scrounging paid), or to patches that did not contain food (scrounging did not pay). Following 5 days of training, differences in the relative use of scrounger were observed between the two groups. Individuals with a productive parent were more likely to scrounge than individuals with a non-productive parent (Katsnelson et al. 2008). However, it is unclear how long such differences would persist, as they were only recorded for 8 days following training. Furthermore, within treatment groups, there was still significant variation among individuals in their use of producer-scrounger alternatives, suggesting that factors other than early experience may influence tactic use decisions.

Another example of experience shaping producer-scrounger tactic use decisions comes from work on zebra finches. Tactic use was compared between individuals that had prior experience with the foraging conditions and individuals that did not, and it was found that prior experience resulted in a higher use of the producer tactic (Beauchamp 2000a). The effect of prior residence likely came about via an effect of increased foraging efficiency. Prior experience with the foraging conditions may allow for better knowledge regarding the distribution of food, which in turn may increase an individual`s foraging efficiency (Beauchamp 2000a). If individuals differ in how long it takes them to locate food patches, then all else being equal, the payoff to producer is greater for individuals that are relatively faster at finding food patches. Individual differences in foraging efficiency related to age (Burger and Gochfeld 1981; Goss-Custard et al. 1998; Steele and Hockey 1995) and food handling rates (Beauchamp 2006) have also been associated with differences in the use of producer-scrounger tactics. Food handling can similarly be expected to influence tactic use. Faster food handling is equivalent to a higher finder`s share, because more food can be consumed before arrival of scroungers at a patch, thereby increasing the payoff to the producer tactic.

Several other factors can be expected to influence tactic use decisions at the level of the individual. For example, the same logic that predicts that higher group level exposure to predation danger may favour higher use of the scrounger tactic can be applied to predict individual differences in tactic use. If using the scrounger tactic provides greater anti-predator benefits, by allowing individuals to occupy safer positions within the flock (Barta et al. 1997; Flynn and Giraldeau 2001; Keys and Dugatkin 1990; Mónus and Barta 2008; Petit and Bildstein 1987) and/or because the scrounger tactic is compatible with anti-predator vigilance (Barbosa 1995; Coolen et al. 2001; Elgar et al. 1986; FitzGibbon 1989; Lima and Bednekoff 1999), then individuals with intrinsically higher vulnerability to predation may have a greater preference for the scrounger tactic.

Similarly, asymmetries between individuals in their energetic state may be an important factor influencing tactic use. The influence of energetic state on variance-sensitive foraging behaviour has largely been studied by comparing individuals during periods of low and high energetic demand, by food depriving individuals in order to increase their energetic requirements, or by altering food availability (reviewed in Bateson and Kacelnik 1998; Kacelnik and Bateson 1996). However, in many species, there are marked inter-individual differences in energy needs (Speakman et al. 2006). For example, basal metabolic rate (BMR), which represents the minimum energy requirement of a non-growing, post-absorptive organism that is at rest in its thermoneutral zone during its normal period of inactivity (McNab 1997), can differ more than 2-fold between individuals of the same species (Speakman et al. 2006). These inter-individual differences are often repeatable over extended periods of time (Bech et al. 1999; Hõrak et al. 2002; Labocha et al. 2004; Rønning et al. 2005) indicating consistent differences in minimum energy requirements of individuals. Because BMR reflects the minimum energy requirement of an individual, individuals with high BMRs should have higher overall energy requirements than individuals with low BMRs (Daan et al. 1990; Ricklefs 1996). Therefore, based on differences in BMR, variance-sensitive foraging theory would predict consistent individual variation in tactic use.

Investigation into the possible role of phenotype-dependent tactic use decisions is warranted as it would have several important implications for producer-scrounger games.

First, given that many of the measures of individual state that are likely to influence tactic use may also be heritable (Blanckenhorn and Hosken 2003; Boag and Alway 1981; Gosler and Harper 2000; Merilä et al. 2001; Phillips and Furness 1998; Rønning et al. 2007), there is the potential for heritability of observed tactic use despite the high degree of flexibility observed in the use of alternative tactics in social foragers. Furthermore, if tactic use is phenotype-dependent, while we would still predict that individuals should choose an allocation strategy whereby both tactics receive equal payoffs, it would not necessarily be the case that the payoffs between individuals would be the same (Davies 1982; Parker 1982; Repka and Gross 1995). Consequently, understanding the role of phenotype in influencing tactic use decisions may provide new insights into individual variation in fitness.

Differences in tactic use resulting from a conditional strategy also imply that the frequency of alternative tactics in a group will vary depending on the specific individuals making up the group (Repka and Gross 1995). Since the payoffs to producer and scrounger alternatives are frequency-dependent (Giraldeau and Caraco 2000; Mottley and Giraldeau 2000), differences in the frequency of tactics between groups would result in differences in intake rates between groups. If tactic use is phenotype-limited, individuals might gauge the condition or tactic use of others in order to join groups of individuals whose use of producer and scrounger tactics best complement their own behavioral profile. Thus, phenotype-limited tactic use may have important implications for group formation decisions.

1.4 Study species: the zebra finch

The zebra finch (*Taeniopygia guttata*) was used as a model system for the experiments described throughout this thesis. Zebra finches are small ground feeding passerine birds, native to Australia (Zann 1996). In the wild, zebra finches form temporary foraging flocks ranging in size from a few to several hundred individuals (Zann 1996). Consequently, zebra finches are likely to use producer-scrounger foraging tactics in their natural setting. Furthermore, previous studies have shown that zebra finches engage in producer-scrounger foraging in the lab (Beauchamp 2000a; Beauchamp 2001; Biondolillo et

al. 1997; Giraldeau et al. 1990), making them a tractable system for manipulative producer-scrounger experiments which may not be possible in the field.

Because zebra finches have been the subject of extensive laboratory and field investigations, much is already known about their biology (Zann 1996). Zebra finches are one of the few systems in which the validity of a commonly used surrogate for fitness, intake rate, has been demonstrated empirically (Lemon 1991). When allowed access to the same quantity of food, zebra finches that were restricted in terms of how quickly they could consume the food (because they had to search for it beneath a layer of seed husks), produced fewer young over their lifetime (Lemon 1991). The zebra finch also offers several advantages for the specific experiments I performed. First, during the breeding season, female zebra finches undergo a large reduction in flight muscle mass, reducing their escape flight performance (Veasey et al. 2001). Flight performance is a major determinant of vulnerability to predation. The large seasonal variation in vulnerability to predation in this species makes it a biologically relevant variable to test as influencing producer-scrounger tactic use (Chapter 2). Second, energetic state is known to be an important factor influencing a range of foraging decisions (Stephens et al. 2007; Stephens and Krebs 1986), and zebra finches have been shown to have consistent individuals differences in energetic requirements (Rønning et al. 2005), differences which are heritable (Rønning et al. 2007). Consequently, zebra finches are ideally suited to testing predictions regarding tactic use decisions for producer-scrounger foraging in relation to energetic state (Barta and Giraldeau 2000; Caraco and Giraldeau 1991) (Chapter 3). Finally, zebra finches are easy to breed in captivity (Zann 1996), which makes it possible to investigate the heritability of individual differences in tactic use (Chapter 4) as well as the effects of relatedness among group members (Chapter 5).

1.5 Thesis overview

In this thesis, I investigate factors that influence tactic use decisions both at the level of the individual, and at the level of the group. In Chapter 2 (published in Behavioral Ecology 2008), I test whether an individual's vulnerability to predation influences tactic use decisions. The scrounger tactic may provide greater anti-predator benefits than the producer tactic

because "scroungers" hop with their heads up and occupy central positions in a group while "producers" hop with their heads down and occupy edge positions. In this chapter, I test whether increasing an individual's vulnerability to predation (using wing-loading manipulations) causes an increased use of the scrounger tactic in zebra finches.

In Chapter 3 (published in Oikos 2009), I test whether individual differences in basal metabolic rate (BMR) are related to individual differences in tactic use. Variance-sensitive producer scrounger models predict that the probability of energetic shortfall will influence tactic use decisions: a higher probability of energetic shortfall early in the day should favour a higher use of the scrounger tactic because it provides more constant rewards compared with the producer tactic (Barta and Giraldeau 2000). BMR represents the minimum energy requirement of an individual (Speakman et al. 2006), and I assumed that higher BMR equates to a higher probability of energetic shortfall, all else being equal. Therefore, I predicted that high BMR individuals would have a higher use of the scrounger tactic than low BMR individuals.

In Chapter 4 (submitted to Behavioral Ecology and Sociobiology), I investigate whether there is evidence that observed tactic use of individuals is heritable. When tactic use is determined under a conditional strategy, observed tactic use may be heritable if the aspects of an individual's state that affect tactic use are themselves heritable (Gross and Repka 1998a; Gross and Repka 1998b). In Chapters 2 and 3, I provide evidence that producer-scrounger tactic use is influenced by individual state, including one state variable which is known to be heritable, BMR (Rønning et al. 2007). In order to test whether tactic use is heritable in zebra finches, full-siblings were placed in different flocks and their use of producer-scrounger tactics was recorded. I tested for family-related differences in tactic use as evidence for heritability of tactic use.

In Chapter 5 (provisionally accepted to Behavioral Ecology), I develop a model to investigate how relatedness influences the SEF of scrounger. Although there has been interest in testing whether relatedness influences the use of producer-scrounger alternatives, there has been no theoretical framework to allow clear predictions to be made (Ha et al. 2003;

McCormack et al. 2007; Tóth et al. 2009). In this chapter, I extend the rate-maximizing producer scrounger model developed by Vickery et al. (1991) to incorporate the inclusive fitness effects of producing and scrounging when foraging with kin versus non-kin. I first consider the situation where increased relatedness among group members alters the propensity to scrounge, and next consider that relatedness may influence both the propensity to scrounge and the propensity to tolerate scrounging. I then test which of these models best predicts the effect of relatedness on social foraging behaviour using a controlled aviary experiment with foraging zebra finches.

Chapter 6 provides a general synthesis of the preceding chapters. The key findings of this thesis are highlighted and discussed in terms their contribution to a broader understanding of producer-scrounger foraging. I also identify some promising directions for future research.

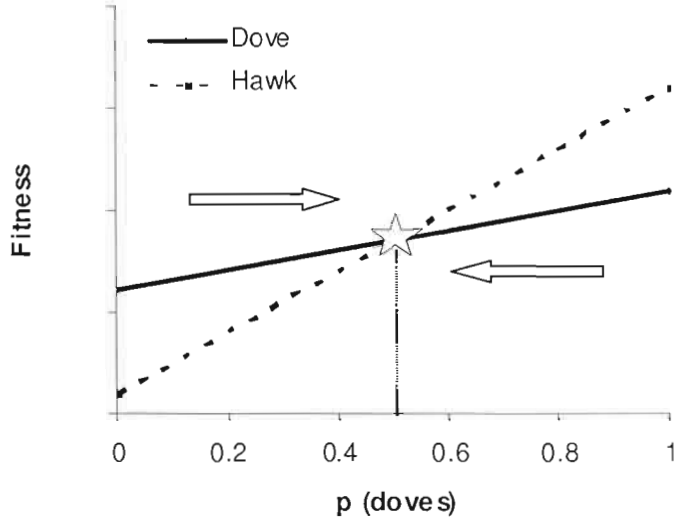

Figure 1.1: Fitness payoffs associated with hawk and dove tactics for different proportions of 'dove' players in the population. The arrows indicate the direction that natural selection will operate. The star indicates the evolutionarily stable strategy (ESS), which in this case occurs at $p_{(dove)} = 0.5$. Altering the value of the resource (R) or cost of fighting (I), will alter the slopes of the lines and change the ESS frequency of dove.

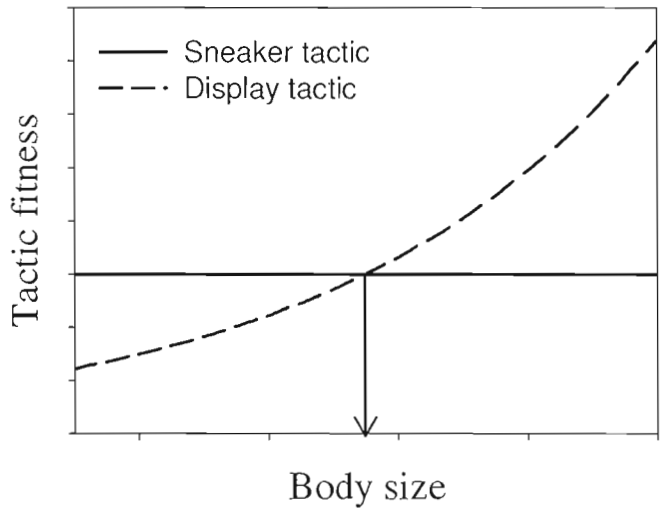

Figure 1.2: Fitness payoffs associated with sneaker and display tactics for males as a function of body size. The arrow indicates the body size switch point: a male smaller than this size maximizes his fitness by playing the sneaker tactic, and a male larger than this size maximizes his fitness by playing the display tactic. Note that fitness will not be equal for individual of different phenotypes (body size) under a strategy that is conditional on phenotype.

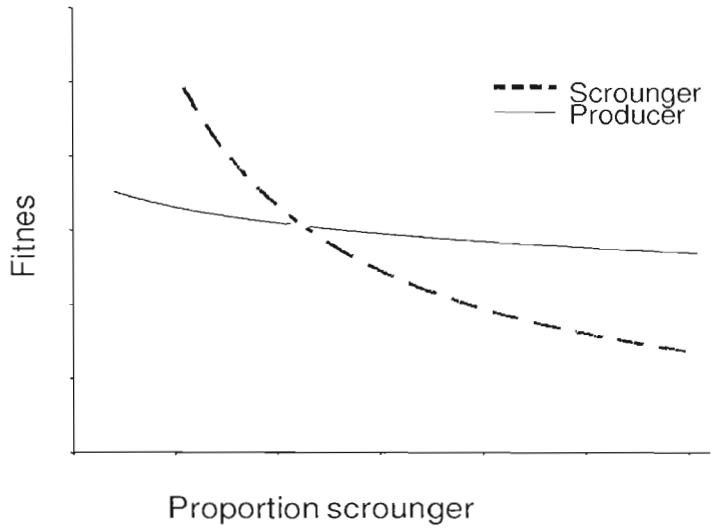

Figure 1.3: Fitness payoffs associated with producer and scrounger tactics at various proportions of scrounger in a group. At low proportions of scrounger tactic use, the fitness payoff from the scrounger tactic is higher, but the payoff from scrounger decreases more rapidly with increasing scrounger frequency than does the fitness payoff of producer. The point where the fitness functions for producer and scrounger intersect is the stable equilibrium frequency (SEF), and the fitness of both producer and scrounger is equal. Adapted from Giraldeau and Caraco (2000).

CHAPTER 2

INCREASING VULNERABILITY TO PREDATION INCREASES PREFERENCE FOR THE SCROUNGER FORAGING TACTIC

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This chapter is presented in the form of an article, published in Behavioural Ecology in 2008 (Volume 19, pages 131-138). Kimberley Mathot was responsible developing the research question, the design and implementation of the experiment, data analysis and writing the manuscript. Luc-Alain Giraldeau provided guidance throughout, and provided comments on the manuscript prior to its submission for publication.

2.1 Abstract

When animals forage in groups, individuals can search for food themselves (producer tactic) or they can search for and join other individuals that have located food (scrounger tactic). The scrounger tactic may provide greater anti-predator benefits than the producer tactic because "scroungers" hop with their heads up and tend to occupy central positions in a group while "producers" hop with their heads down and tend to occupy edge positions. We tested whether increasing an individual's vulnerability to predation (using wing loading manipulations) causes an increased preference for the scrounger tactic in zebra finches (*Taeniopygia guttata*). Wing loading manipulations were effective at increasing the focal individual's perception of vulnerability to predation; treatment individuals increased their total time allocated to vigilance, while control individuals did not. Treatment individuals also increased their use of the scrounger tactic (proportion of hops with head-up) and scrounged a greater proportion of patches, while control individuals exhibited no changes. Our results are consistent with the hypothesis that the scrounger tactic confers greater anti-predator benefits than the producer tactic, although whether anti-predator benefits are achieved through differences in head orientation, spatial position, or both, remains unclear. Our finding that individuals adjust their use of the scrounger tactic according to changes in their phenotype provides evidence for phenotype-limited allocation strategies in producer-scrounger games.

2.2 Introduction

Animals foraging in groups can search for feeding opportunities themselves (producer tactic) or they can search for opportunities to exploit the food discoveries of conspecifics (scrounger tactic). Both tactics are maintained in the group via negative-frequency dependence because 'producer' does better relative to 'scrounger' when 'producer' is rare, and vice versa (Mottley and Giraldeau 2000; Vickery et al. 1991). The stable equilibrium frequency (SEF) of tactic use within a group is defined as the point where no individual can increase its fitness via a unilateral shift in tactic use (Mottley and Giraldeau 2000). Several factors influence where the SEF of a group lies, including patch distribution (Livoreil and Giraldeau 1997; Vickery et al. 1991), the extent to which the resource can be monopolized by the producer (Mottley and Giraldeau 2000), and group size (Coolen 2002; Vickery et al. 1991).

Most producer-scrounger foraging models predict the SEF level of investment in each tactic for the group, but make no predictions regarding how each individual within the group should contribute to this SEF (Barnard and Sibly 1981; Giraldeau and Caraco 2000; Vickery et al. 1991). At the SEF, marked, yet long-lived inter-individual differences in the relative use of alternative tactics may exist, so long as the SEF is met overall (Barta et al. 2004; Beauchamp 2001; Bugnyar and Kotrschal 2002; Ha and Ha 2003). Furthermore, individual differences may be maintained across different contexts (Beauchamp 2001; Koops and Giraldeau 1996), indicating that tactic use decisions may also be phenotype-limited. Therefore, more recent empirical models of producer-scrounger foraging have attempted to include phenotypic constraints on tactic use (Ranta et al. 1998; Ranta et al. 1996). Social dominance rank and foraging efficiency in particular have been studied explicitly with respect to individual differences in tactic use (Barta and Giraldeau 1998; Beauchamp 2006; Giraldeau et al. 1990; Liker and Barta 2002; Thibaudeau 2004). However, many of the factors that have been hypothesized to influence group level investment in alternative tactics could equally be expected to influence individual tactic use decisions.

Here, we test whether an individual's vulnerability to predation influences its allocation to producer-scrounger foraging tactics. Predation danger has previously been considered as a potential factor influencing producer-scrounger tactic use at the level of the group. Individuals using the scrounger tactic tend to hop with the head oriented upwards (Coolen et al. 2001), and several studies have demonstrated that individuals that use foraging behaviours with a head-up orientation have greater inherent vigilance compared with those that use more head-down foraging behaviours (Barbosa 1995; Elgar et al. 1986; FitzGibbon 1989; Lima and Bednekoff 1999). In fact, disproportionately greater investment in vigilance for predators by scroungers has been suggested as a possible mechanism promoting the tolerance of scroungers within groups by producers, despite their negative effect on foraging intake rate (Ranta et al. 1998). Furthermore, 'scroungers' are more likely to be found in central positions in the group (Barta et al. 1997; Flynn and Giraldeau 2001), which tend to be safer compared with edge positions (Elgar 1989; Keys and Dugatkin 1990). Therefore, theoretical models have predicted that increased predation danger should increase the SEF of the scrounger tactic in the group (Barta and Giraldeau 2000). However, studies testing this prediction have yielded contradictory results. In northwestern crows (*Corvus caurinus*), the presence of predators had no effect on scrounger tactic use (Ha and Ha 2003). Similarly, in flocks of nutmeg mannikins (*Lonchura punctulata*), experimentally increasing the perceived risk of predation by increasing the distance between the foraging site and protective cover had no effect on the relative use of the scrounger tactic (Coolen and Giraldeau 2003). In contrast, studies in free ranging ravens (*Corvus corax*) (Bugnyar and Kotrschal 2002), and tree sparrows (*Passer montanus*) (Barta et al. 2004), reported higher use of scrounger tactics in groups foraging under increased predation risk, although in both cases, mechanisms other than anti-predator benefits of scrounging may have accounted for the shift.

Therefore, it remains unclear to what extent the use of the scrounger tactic may confer the individual that uses it greater anti-predator benefits compared with the use of producer. If either head orientation or spatial position in a group influences predation risk, then differences among individuals with respect to vulnerability to predation are likely to influence tactic use decisions. We used a paired repeated measures design to test whether the use of producer and scrounger tactics at the level of the individual is mediated by

vulnerability to predation. We experimentally increased the vulnerability to predation of focal individuals using wing loading manipulation, while control individuals received sham manipulations. Wing loading, defined as mass per unit area of wing, is related to escape performance; higher wing loading reduces escape performance (Bednekoff 1996; Bednekoff and Houston 1994; Pennycuick 1975; Pennycuick 1989). Therefore, we used wing area reduction to increase experimentally an individual's vulnerability to predation. We predict that if scrounging provides greater anti-predator benefits compared with producing, then an experimental increase in wing loading should lead to an increase in an individual's relative use of the scrounger tactic.

2.3 Methods

2.3.1 Study subjects and aviaries

Commercially purchased zebra finches (*Taeniopygia guttata*) were maintained on a 12h:12h light:dark cycle (lights on from 6h00 to 18h00) at temperatures between 22 and 24°C in same-sex groups with ad libitum access to water at all times. Outside of experimental periods, the birds were housed together in cages (113 × 61 × 90 cm high) with ad libitum access to vitamin-supplemented commercial millet seed mixture.

During experiments, 8 flocks of 8 randomly selected birds from a colony of 54 female zebra finches, were placed into an indoor aviary (1.5 × 3.8 × 2.3 m high). We used female-only groups because female birds undergo large fluctuations in wing-loading during egg laying and incubation (Kullberg et al. 2005; Moreno 1989; Veasey et al. 2001), making manipulations of wing-loading a biologically relevant treatment for females. Some individuals were used in more than one group, however, a single, randomly selected, focal individual was observed per flock and focal individuals were never used in more than one group. Each bird was identified with a unique combination of 2-4 color leg bands.

Each aviary contained two large perches and a foraging grid that consisted of 2 side by side plywood boards with a combined dimension of 2.0 by 1.2 m, in which a total of 198

wells 1.3 cm in diameter, 0.8 cm deep, and spaced at 10 cm intervals were drilled. Foraging grids were placed on tables approximately 90 cm above the aviary floor, which allowed a seated observer to videotape the birds through a one-way mirror using a 8 mm color camcorder mounted on a tripod. The foraging grid was covered by a sheet of black plastic at all times except during the foraging trials. The perches were placed at the far end of the aviary so that birds could not see directly into the wells from the perches, but had to fly down to the foraging grid to search for food.

2.3.2 Experimental procedure

Birds were given 2 d to become familiar with the aviaries. Food was removed at 18h00 on the evening of the second day, and each evening thereafter (evenings 2 through 10). Trials commenced at 8h30 the following mornings (days 3 through 11). Thus, the birds were deprived of food during the 12h dark phase, plus an additional 2.5h after lights on, durations that were necessary given that they store seeds in their extensible crops for overnight use.

Foraging trials were conducted for 9 d (days 3 through 11) 5 times per d at 1 h intervals. During each foraging trial, 10 millet seeds were placed in each of 15 randomly selected wells. Trials typically lasted circa 5 min, after which time, all the patches on the foraging grid had been exploited and the birds returned to the perches. Birds were given ad libitum access to food following the final foraging trial each day (from 12h40 to 18h00).

The first 3 d of foraging trials (days 3 - 5) were used to train the birds on the seed distribution, and were not videotaped. The following 6 d of foraging trials were videotaped as the observer (KJM) called out the location of individuals into the audio channel of the videotape recorder to facilitate the identification of the focal individual during the playbacks from which data were recorded. Days 6 - 8 provided pre-manipulation behaviour levels and days 9-11 provided post-manipulation levels. Manipulations were carried out after the last foraging trial of day 8, with groups being randomly assigned to either experimental ($n = 4$) or control ($n = 4$) treatments.

Body mass was measured once a day at either 07h30, 12h40, or 18h00 by placing the bird in a paper bag and weighing it on a digital balance to 0.01 g. The weighing time of day for each bird was randomized on condition that every three days, each focal bird was weighed once at each of the three time periods.

2.3.3 Manipulation of vulnerability to predation

Prior to the start of experiments, digital photographs were taken of each focal bird's right wing, stretched in a standardized manner over a sheet of white paper on which a $1cm^2$ area was clearly identified. Individuals randomly assigned to be in the experimental treatment had the tips of their 5 outer primary feathers of both wings clipped circa 5 mm, and their right-wing re-photographed in the same manner as described above. Individuals assigned to the control treatment were handled in the same way, but received sham feather clippings.

Digital photographs were analyzed using GNU Image Manipulation Program 2 (http://www.gimp.org) to calculate the surface area of the right wing in cm^2. Photograph files were coded so as not to reveal the identity or treatment of the subject, although individuals assigned to the experimental treatment were obvious post-manipulation because their wing tips were blunt following feather clipping. Total wing area was estimated as twice the surface area of the right wing. Wing loading was calculated as: average body mass value during foraging trials ($[mass_{07h30} + mass_{12h40}] / 2$) divided by the estimated total wing area (right wing area $\times$ 2) for both pre- and post-manipulation wing areas and mass values.

2.3.4 Video analysis

Data was recorded from the first 1 min of observations of video playbacks of trials playing at 1/5 speed using Noldus Observer 5.0 Video Pro. Videos were observed in random sequence by an observer that was blind to the treatment condition. The following behaviours were recorded: hop with head up, hop with head down, produce patch, scrounge patch, scanning, off grid, and others.

Hopping with head up was defined as all jumps made with the head oriented such that a line drawn from the eyes through the nares would be parallel to the horizon or higher. When the projected line was below the horizon, the focal individual was scored as hopping with the head down. An individual was scored as having produced a patch when it was the first to encounter and feed at a patch. Individuals that moved rapidly towards a patch with at least one other bird already there were scored as scrounging the patch, irrespective of whether it subsequently fed from the patch or not. Scanning was scored when a stationary bird held its head up. All time spent off the foraging grid (on the perches, on the table, or on the floor beneath the table) was recorded. All other behaviours were pooled together as 'others'. For each trial the following values were calculated: scanning rate (number of scans / min on foraging grid), mean scan duration, proportion of time spent scanning, proportion of hops with the head up (hops with head up / [hops with head up + hops with head down]), and proportion of patches scrounged (no. patches scrounged / [no. patches produced + no. patches scrounged]). Proportion data were arcsine square root transformed prior to statistical analyses.

2.3.5 Statistical analyses

Separate paired t-tests were carried out on the wing area and wing loading values obtained before and after manipulations for both control and experimental birds. Although we had *a priori* expectations regarding the direction of change in wing area and wing loading values for experimental birds (decreased wing area and increased wing loading), we present the more conservative two-tailed statistics. Tests for control birds were also two-tailed.

Body mass values were compared within individuals before and after manipulations using a four-stage nested factorial analysis (Montgomery 2005). The random effect, 'ID', was nested within treatment, while all fixed effects ('treatment', 'observation period' and 'time of day') occurred in a factorial design.

Behavioural data (scans / min, mean scan duration, proportion of time scanning, proportion of hops with head up, proportion of patches joined) were analyzed using three-

stage nested-factorial designs (Montgomery 2005). The random factor, ID, was nested within treatment type, while treatment type and observation period were arranged in a factorial. Full models are provided in Tables 1 and 2.

We used a paired experimental design because the high variation in tactic use between individuals means that very large samples of individuals would be required to detect differences between groups of different individuals. Using a paired-design, each individual served as its own control, increasing our power to detect an effect of treatment with modest sample sizes. Because background values of tactic use were always obtained from treatment individuals prior to manipulation, control individuals were necessary in order to demonstrate that changes in tactic use among treatment individuals were not the result of some temporal effect. Therefore, the critical test given our experimental design is whether the change in tactic use between pre- and post- observation periods varies depending on the treatment type received (treatment × observation period). Because statistical tests have reduced power to detect significant interactions (Littell et al. 1991), Tukey HSD post-hoc tests controlling for multiple comparisons were used to test for 1) the effect of manipulation on experimental birds, and 2) the effect of sham-manipulations on control birds wherever the 'treatment × observation period' interaction had a $p < 0.10$. In all cases, models included significant nested effects. However, as we are not interested in differences due to individuals, results for these effects are not discussed further. Values presented throughout the text are means ± standard errors.

2.4 Results

2.4.1 Wing area, body mass, and wing loading

The total wing area of birds prior to wing area manipulations varied from 30.37 to 37.13 cm^2. Wing area manipulations significantly reduced the wing area of experimental (two-tailed paired t-test, t-ratio = 5.45, $p = 0.012$) but not control (two-tailed paired t-test, t-ratio 1.34, $p = 0.27$) individuals. Wing area decreased by 13.45 ± 2.39% (range 10.72 to

20.58%) in experimental individuals, compared with 1.20 ± 0.91% (range -0.61 to 3.18%) in control individuals.

There were no significant interactions between treatment, observation period, or time of day (all $p > 0.30$) for body mass. Body mass did not differ between treatment types ($F_{1,6} = 1.65$, $p = 0.25$). However, body mass did differ according to time of day ($F_{2,12} = 96.88$, $p < 0.0001$) and observation period ($F_{1,6} = 15.39$, $p = 0.0078$) (Figure 2.1). Within observation periods, body mass did not differ significantly between 07h30 and 12h40 measurements (Tukey's test: $Q = 2.67$, $p > 0.05$), but was significantly higher at 18h00 (Tukey's test: $Q = 2.67$, $p < 0.05$), just after the period of ad libitum feeding. For a given time of day, body mass measures were higher in the post-manipulation phase of the experiments.

The combined effect of changes in body mass and wing area resulted in a 19.51 ± 3.89% (range 12.55 to 30.65%) increase in wing loading for experimental birds (Figure 2.2). The effect was significant (two-tailed paired t-test, t-ratio = 5.52, $p = 0.011$). Although the increase in body mass between pre- and post-manipulation phases of the experiment meant that wing loading tended to increase also in control individual following manipulations (mean increase 5.5 ± 3.14 %, range -0.11 to 11.62%), this effect was not significant (two-tailed paired t-test, t-ratio = 1.73, $p = 0.18$).

2.4.2 Scanning and scrounging behaviour

There was no interaction between observation period (pre- or post-manipulation) and treatment type for scanning rates (treatment×observation period: $F_{1,6} = 1.19$, $p = 0.32$) (Table 2.1, Figure 2.3*a*). Scanning rates increased from 18.89 ± 1.06 to 22.10 ± 1.06 scans/min following either control or experimental manipulation ($F_{1,6} = 27.90$, $p < 0.01$). Within each observation period, there were no differences in scanning rates between control and experimental individuals ($F_{1,6} = 0.05$, $p = 0.82$).

There was a significant interaction between observation period (pre- or post-manipulation) and treatment type for mean scan duration (treatment×observation period: $F_{1,6}$

= 10.44, p = 0.02) (Table 2.1, Figure 2.3*b*). Post-hoc analyses indicate that experimental individuals significantly increased their mean scan duration following manipulation (Tukey's test: Q = 3.46, $p < 0.05$), from 0.43 ± 0.07 to 0.54 ± 0.07 s, a 25% increase in mean scan duration. There was no change in the mean scan duration of control individuals (Tukey's test: Q = 3.46, $p > 0.05$).

The effect of observation period (pre- or post-manipulation) on the proportion of time spent scanning also differed as a function of treatment type (treatment×observation period: $F_{1,6} = 6.54$, p = 0.04) (Table 2.1, Figure 2.3*c*). Post-hoc analyses indicate that experimental individuals significantly increased the proportion of time spent scanning after wing manipulation (Tukey's test: Q = 3.46, $p < 0.05$), from 0.13 ± 0.03 to 0.20 ± 0.03, a 50% increase in time allocated to scanning. In contrast, there was no change in the proportion of time spent scanning among control individuals (Tukey's test: Q = 3.46, $p > 0.05$).

Differences in the proportion of hops with head up between pre- and post-manipulation phases of the experiment differed according to treatment (treatment × observation period: $F_{1,6} = 4.99$, p = 0.067) (Table 2.2, Figure 2.4). The wing loading manipulation resulted in a significant increase in the proportion of hops with the head up in experimental individuals (Tukey's test: Q = 3.46, $p < 0.05$), from 0.32 ± 0.12 to 0.48 ± 0.12, a 50% increase in scrounger tactic use. In contrast, manipulations had no effect on scrounger tactic use in control individuals (Tukey's test: Q = 3.46, $p > 0.05$).

Similarly, differences in the proportion of patches scrounged between pre- and post-manipulation phases of the experiment differed according to treatment (treatment × observation period: $F_{1,6} = 11.38$, p = 0.015) (Table 2.2, Figure 2.5). Coincident with the increased use of 'hopping with head up', there was also an increase in the proportion of patches scrounged in experimental individuals following manipulation (Tukey's test: Q = 3.46, $p < 0.05$), from 0.56 ± 0.08 to 0.73 ± 0.08. Again, manipulations had no effect on the proportion of patches scrounged in control individuals (Tukey's test: Q = 3.46, $p > 0.05$).

2.5 Discussion

We tested whether changes in an individual's perceived vulnerability to predation influence its allocation decision to alternative social foraging tactics. We found that increased wing loading significantly increased an individual's perception of vulnerability, as evidenced by the increase in proportion of time spent scanning in experimental individuals following manipulations, compared with control individuals, who showed no change in time allocated to scanning. Experimentally manipulated individuals also increased their investment in the scrounger tactic and consequently scrounged a greater proportion of patches than controls. These results are consistent with the hypothesis that scrounger provides greater anti-predator benefits than producer. Furthermore, the finding that changes in the condition of an individual influences its use of producer or scrounger shows that these decisions can be phenotype-limited.

Increased-wing loading has been reported to increase vulnerability to predation in various avian species (Burns and Ydenberg 2002; Kullberg et al. 2005; Marchetti et al. 1995). Recently however, some authors have called into question whether or not natural variation in wing loading influences predator escape performance, given that most studies that have reported an effect have manipulated wing loading beyond the usual range found in natural populations (van der Veen and Lindström 2000). Although the magnitude of our wing loading manipulation is large (circa 20% increase), it remains well within the scale of changes in wing loading that would be experienced by female birds during egg laying (Kullberg et al. 2005; Moreno 1989; Veasey et al. 2001). Furthermore, the magnitude of change induced within individuals is of a comparable magnitude to the natural variation that exists among individual zebra finches (Hambly et al. 2002).

Our finding that birds with experimentally increased wing loading showed increases in mean scan duration and proportion of time spent scanning, are indicative of increased wing loading resulting in an increased perception of vulnerability to predation. Although control birds neither increased their mean scan duration nor proportion of time spent scanning, we did record an increase in scanning rate among our control birds following manipulation. It is

not clear why control birds increased their scanning rates during the post-manipulation phase of the experiment, however, regular disturbance in the aviaries while carrying out the experiments (entering to place seeds in the foraging grids, removing food at night, and capturing birds for daily mass measurements), may have resulted in a general increase in weariness throughout the experiments for both control and experimental birds, irrespective of treatment type. However, the magnitude of the increase in scanning rate was small (< 3 additional scans per minute), and did not result in any increase in the time invested in scanning behaviours. Therefore, given that only experimental birds showed an increase in mean scan duration and proportion of time spent scanning, we conclude that the change in perceived vulnerability to predation was significantly greater in experimental birds than control birds following wing loading manipulations.

We predicted that vulnerability to predation might influence individual allocation strategies to producer and scrounger foraging tactics. When individuals use the producer tactic, they tend to hop with the head oriented downwards, and are more likely to be found on the periphery of their foraging group, compared with scroungers, which hop with their heads oriented upwards (Coolen et al. 2001) and tend to occupy central positions in the group (Barta et al. 1997; Flynn and Giraldeau 2001). Both head orientation while foraging and position within a group can influence vulnerability to predation. More head up foraging behaviours have been demonstrated to provide increased predator detection abilities compared with head down foraging behaviours in several species (Barbosa 1995; Elgar et al. 1986; FitzGibbon 1989; Krause and Godin 1996; Lima and Bednekoff 1999). Also, birds occupying central positions in flocks are less likely to be captured by predators (Keys and Dugatkin 1990; Petit and Bildstein 1987).

Consistent with our predictions, experimental birds significantly increased their use of the scrounger tactic use (hopping with the head up), resulting in a larger proportion of scrounged patches (50% and 30% increase respectively), whereas no change was observed in control birds. Although we attribute this shift in tactic use to the increased perceived vulnerability to predation of experimental birds, an alternative explanation for the increased use of the scrounger tactic is that the wing-loading manipulations may have resulted in an

increased energy expenditure among experimental birds due to higher energetic cost of flight with increased wing-loading (Pennycuick 1975; Pennycuick 1989). However, if increased energy expenditure leads to a decreased probability of meeting daily energy requirements, then we would predict a shift towards increased use of the producer tactic among experimental birds (Koops and Giraldeau 1996). Therefore, we conclude that increased perceived vulnerability to predation remains the most likely explanation for the increased use of scrounger tactic in experimental birds.

Our results differ from those of both Coolen and Giraldeau (2003) and Ha and Ha (2003) who report no effect of predation danger on the SEF of scrounging in nutmeg mannikins and north-western crows, respectively. However, in both those studies, the whole group was exposed to variations in predation danger. When all group members simultaneously experience an increase in predation danger, they cannot all increase their use of scrounger without suffering a concomitant decline in foraging returns resulting from overuse of the scrounger tactic within the group. It is possible that balancing foraging returns and predation danger concurrently mitigates the effects of increasing predation danger on the group's mean use of the scrounger tactic. Our manipulations altered the condition of a single individual per flock of eight birds and therefore would have influenced to a relatively smaller degree the foraging pay-offs to the scrounger tactic and hence the group's use of tactics. We argue that differences between our results and those of Coolen and Giraldeau (2003) and Ha and Ha (2003) highlight the importance of differentiating between group level effects and effects at the level of the individual in frequency-dependent games.

Increased incidence of scrounging under higher predation danger have nonetheless been reported in both sparrows (Barta et al. 2004) and ravens (Bugnyar and Kotrschal 2002). However, alternative explanations such as risk-sensitive foraging or differences in the identity of individuals feeding in the different habitats may also have accounted for the observed increased scrounging. Our study provides unambiguous evidence that increasing an individual's (as opposed to a group's) vulnerability to predation increases the individual's preference for the scrounger tactic. However, our experimental design does not enable us to determine whether the anti-predator benefits of scrounging are derived from compatibility

between scrounging and anti-predator vigilance, the spatial position of scroungers within groups, or both. Experiments controlling for the differences in head orientation between tactics are necessary to tease apart these effects.

To date, relatively little is known about the factors influencing inter-individual differences in social foraging tactic use (Beauchamp 2000a; Beauchamp 2001; Thibaudeau 2004). We show that individuals adjust their investment in alternative social foraging tactics according to changes in their phenotype, which suggests that inter-individual differences in phenotype may also influence individual tactic use decisions. While most studies of producer-scrounger foraging have considered variations in factors at the level of the group, our results demonstrate that the effect of a given factor on tactic use can differ depending on the level at which the factor operates (group or individual). We suggest that phenotype-limited games may be more prevalent than previously suspected, even among groups of similar sized and socially egalitarian individuals.

2.6 Acknowledgements

We thank Pedro Peres-Neto and Denis Réale for statistical advice, and two anonymous referees for comments. These experiments conform to guidelines of the Canadian Council for Animal Care and were approved by the University Animal Care Committee. KJM was financially supported by a Natural Sciences and Engineering Research Council (NSERC, Canada) scholarship and the research was supported by an NSERC Discovery Grant to LAG.

Table 2.1: Three-stage nested-factorial analysis results for measures of vigilance.

Source of variation	SS	MS	DF	F	P
A. Dependent variable: Scans/min					
treatment	13.1712	13.1712	1	0.0536	0.8246
observation period	616.237	616.237	1	27.8955	0.0019
ID(treatment)-Random	1474.69	245.782	6	11.1259	0.0049
observation period × treatment	26.2663	26.2663	1	1.1890	0.3174
observation period × ID(treatment)-Random	132.546	22.0909	6	0.8353	0.5437
Error	5924.0344	26.447	224		
B. Dependent variable: Mean scan duration (s)					
Treatment	0.00697	0.00697	1	0.0112	0.9191
observation period	0.11284	0.11284	1	3.6635	0.1041
ID(treatment)-Random	3.72873	0.62146	6	20.1767	0.0010
observation period × treatment	0.3216	0.3216	1	10.4414	0.0179
observation period × ID(treatment)-Random	0.1848	0.0308	6	1.4039	0.2141
Error	4.91459	0.02194	224		
C. Dependent variable: arcsine sqrt proportion of time scanning					
treatment	0.00439	0.00439	1	0.0199	0.8923
observation period	0.1938	0.1938	1	14.5572	0.0088
ID(treatment)-Random	1.32142	0.22024	6	16.5428	0.0017
observation period × treatment	0.08713	0.08713	1	6.5444	0.0430
observation period × ID(treatment)-Random	0.07988	0.01331	6	1.9663	0.0715
Error	1.51663	0.00677	224		

Table 2.2: Three-stage nested-factorial analysis results for proportion of hops with head up and proportion of patches joined.

Source	SS	MS	DF	F Ratio	P
A. Dependent variable: arcsine sqrt proportion of hops with head up					
treatment	0.8454	0.8454	1	0.2032	0.6680
observation period	0.7290	0.7290	1	7.5232	0.0336
ID(treatment)-Random	24.9570	4.1595	6	42.9229	0.0001
observation period × treatment	0.4835	0.4835	1	4.9891	0.0669
observation period × ID(treatment)-Random	0.5814	0.0969	6	2.2168	0.0425
Error	9.7921	0.0437	224		
B. Dependent variable: arcsine sqrt proportion of patches scrounged					
treatment	0.5788	0.5788	1	0.1388	0.7223
observation period	0.7850	0.7850	1	10.3824	0.0181
ID(treatment)-Random	25.0275	4.1713	6	55.1677	<.0001
observation period × treatment	0.8607	0.8607	1	11.3830	0.0150
observation period × ID(treatment)-Random	0.4537	0.0756	6	0.7010	0.6491
Error	24.1602	0.1079	224		

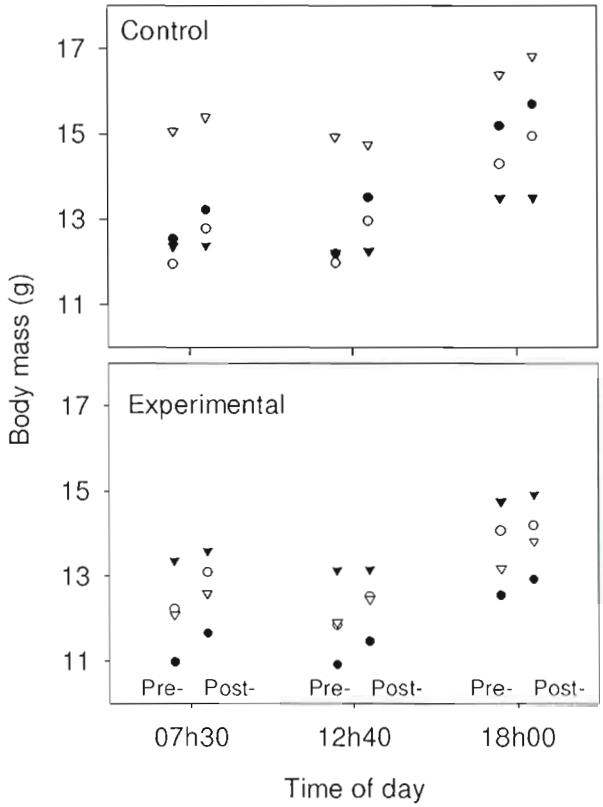

Figure 2.1: Body mass as a function of time of day, observation period, and treatment. Each symbol represents a separate focal individual. Pre- and post-manipulation mass values are offset from one another for clarity.

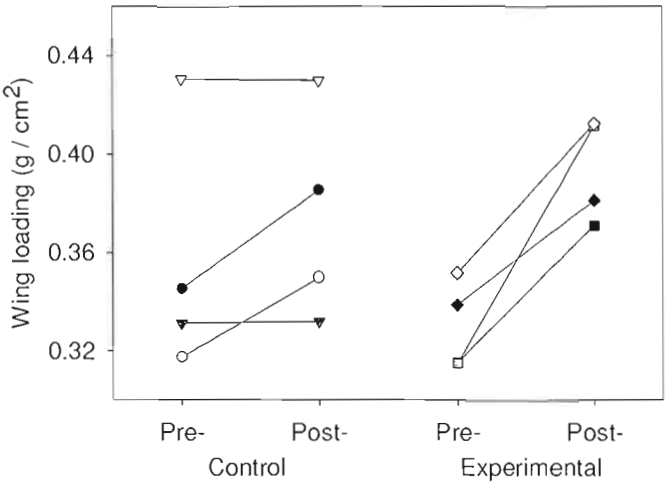

Figure 2.2: Wing loading (g / cm^2) values for control and experimental treatments, pre- and post-manipulation. Each symbol represents a different focal individual

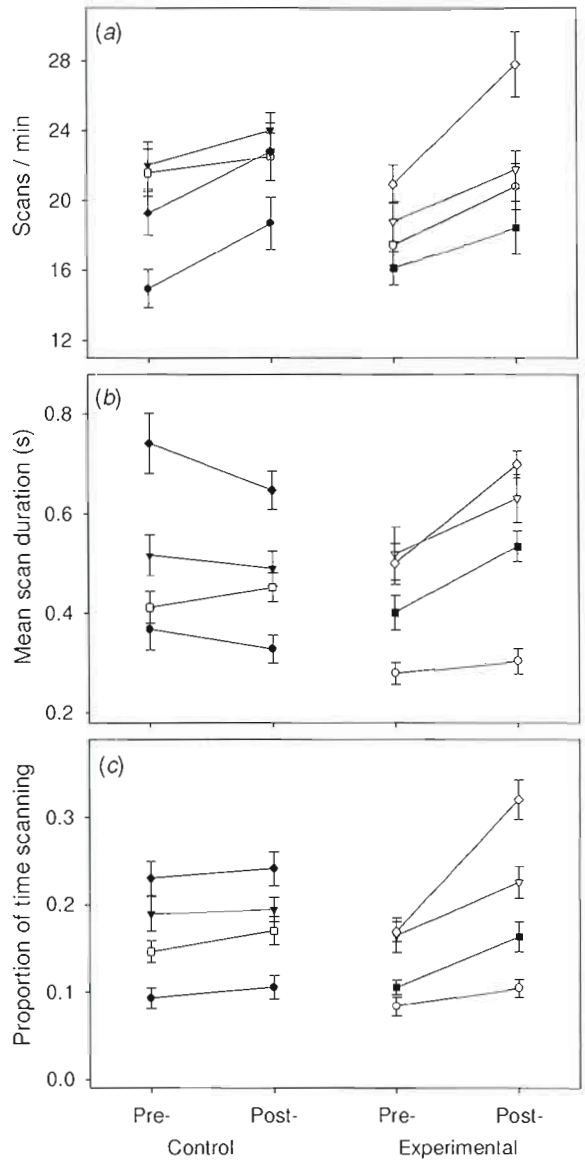

Figure 2.3: (*a*)Scanning rate (scans/min), (*b*) mean scan duration (sec), and (*c*) proportion of time spent vigilant for control and experimental focal individuals both before (pre-) and after (post-) manipulations. Each symbol and associated error bars represent the mean and s.e. for a different focal individual. Lines connect the pre- and post- values for the same individual. Note that graph depicts raw data, while statistical analyses were carried out on arcsine square root transformed values of the proportion data.

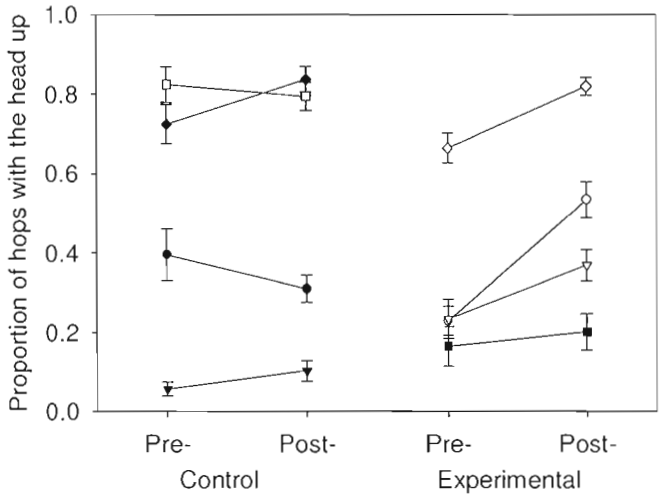

Figure 2.4: Proportion of hops with head up for control and experimental focal individuals both before (pre-) and after (post-) manipulations. Each symbol and associated error bars represent the mean and s.e. for a different focal individual. Lines connect the pre- and post-values for the same individual. Note that graph depicts raw data, while statistical analyses were carried out on arcsine square root transformed data.

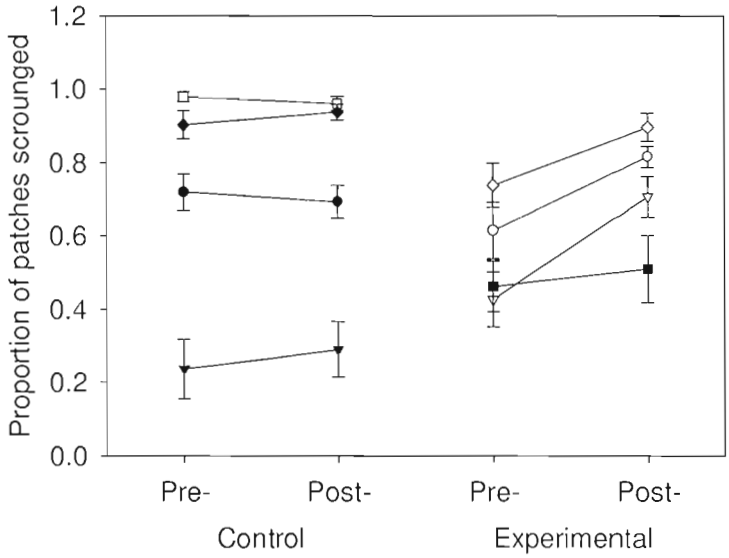

Figure 2.5: Proportion of patches joined for control and experimental focal individuals both before (pre-) and after (post-) manipulations. Each symbol and associated error bars represent the mean and s.e. for a different focal individual. Lines connect the pre- and post- values for the same individual. Note that graph depicts raw data, while statistical analyses were carried out on arcsine square root transformed data.

PREAMBLE

In the previous chapter, we showed that individual vulnerability to predation influences tactic use decisions. Higher individual vulnerability to predation favours a higher use of the scrounger tactic. Thus, inter-individual variation in vulnerability to predation may account for at least part of the observed inter-individual differences in tactic use. However, the energetic state of individuals is also known to be an important factor influencing a range of foraging decisions. In this chapter, we test whether natural variation in the basal metabolic rate (BMR) of individuals influences their use of producer and scrounger tactics.

This chapter is presented in the form of an article, published in Oikos in 2009 (Volume 118, pages 545-552). Kimberley Mathot was responsible for developing the research question, the experimental design, much of the data collection, data analysis and writing of the paper, with supervision from Luc-Alain Giraldeau. Don Thomas loaned the respirometry equipment for measuring basal metabolic rate, Vincent Careau set up the respirometry equipment and demonstrated to Kimberley Mathot how to carry out BMR measurements, and Sophie Godde helped with some of the behavioural data collection. All co-authors read and provided feedback on the manuscript prior to it being submitted for publication.

CHAPTER 3

TESTING DYNAMIC VARIANCE-SENSITIVE FORAGING USING INDIVIDUAL DIFFERENCES IN BASAL METABOLIC RATES OF ZEBRA FINCHES

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3.1 Abstract

Social foragers can alternate between searching for food (producer tactic), and searching for other individuals that have located food in order to join them (scrounger tactic). Both tactics yield equal rewards on average, but the rewards generated by producer are more variable. A dynamic variance-sensitive foraging model predicts that social foragers should increase their use of scrounger with increasing energy requirements and/or decreased food availability early in the foraging period. We tested whether natural variation in minimum energy requirements (basal metabolic rate or BMR) is associated with differences in the use of producer-scrounger foraging tactics in female zebra finches (*Taeniopygia guttata*). As predicted by the dynamic variance-sensitive model, high BMR individuals had significantly greater use of the scrounger tactic compared with low BMR individuals. However, we observed no effect of food availability on tactic use, indicating that female zebra finches were not variance-sensitive foragers under our experimental conditions. This study is the first to report that variation in BMR within a species is associated with differences in foraging behaviour. BMR-related differences in scrounger tactic use are consistent with phenotype-dependent tactic use decisions. We suggest that BMR is correlated with another phenotypic trait which itself influences tactic use decisions.

3.2 Introduction

Energetic state is an important factor influencing foraging decisions in animals (Stephens and Krebs 1986). When faced with increased energy demands or an increased probability of energetic shortfall, many animals will increase their time allocated to foraging (Turpie and Hockey 1993), accept greater predation danger while foraging (Lima and Dill 1990) or adopt different foraging tactics (Stephens and Krebs 1986). Changes in foraging tactic use can occur under increased energy requirements due to changes in the forager's preference or aversion to variance, and hence uncertainty, in the food reward associated with a given foraging tactic. Variance-sensitive foragers act to minimize the probability of energetic shortfall.

Predictions from static models of variance-sensitive foraging are captured by the now famous energy-budget rule: be variance-averse when expected energy budget is positive, be variance-prone when expected energy budget is negative (Stephens 1981). However, this rule is based on a static analysis that does not take into account the remaining time horizon when the decision must be made. Dynamic state-dependent models of variance-sensitive foraging are often better predictive devices because they expect that an individual's preference or aversion to variance depends both on its energetic state and the time available in the foraging period to reach its energetic requirement (Barta and Giraldeau 2000; Houston and McNamara 1999) (Figure 3.1). When expecting an energetic shortfall, animals should prefer more variable outcomes if they have only a short time remaining in the foraging period (Barta and Giraldeau 2000; Caraco and Giraldeau 1991). However, animals expecting an energetic shortfall but with much time remaining in the foraging period, should favour the tactic that provides more certain rewards, and avoid variance (Barta and Giraldeau 2000). In this study we propose to test predictions of a dynamic variance-sensitive model.

The influence of energetic state on variance-sensitive foraging behaviour has largely been studied by comparing individuals during periods of low and high energetic demand, by food depriving individuals in order to increase their energetic requirements, or by altering food availability (for reviews see Bateson and Kacelnik 1998; Kacelnik and Bateson 1996).

However, in many species, there are marked inter-individual differences in energy needs (Speakman et al. 2006). For example, basal metabolic rate (BMR), which represents the minimum energy requirement of a non-growing, post-absorptive organism that is at rest in its thermoneutral zone during its normal period of inactivity (McNab 1997), can differ more than 2-fold between individuals of the same species (Speakman et al. 2006). These inter-individual differences are often repeatable over extended periods of time (Bech et al. 1999; Hõrak et al. 2002; Labocha et al. 2004; Rønning et al. 2005) indicating consistent differences in minimum energy requirements of individuals.

Here we ask whether individual differences in BMR within a species are associated with differences in the use of high- or low-variance foraging tactics in a group foraging context. We use a group foraging context because when individuals forage in groups they can alternate between two foraging tactics; actively searching for food (producer tactic), or searching for other group mates that have located food in order to join them (scrounger tactic) (Barnard and Sibly 1981; Giraldeau and Caraco 2000). Both tactics are maintained in groups via negative frequency-dependence because producer does better relative to scrounger when producer is rare, and vice versa (Mottley and Giraldeau 2000; Vickery et al. 1991). The stable frequency of tactic use exists at the point where no individual can increase its fitness via a unilateral shift in tactic use (Mottley and Giraldeau 2000). Although the mean payoff to each tactic is the same within groups at equilibrium, the variance, and hence uncertainty of payoff, is greater for producer than for scrounger (Lendvai et al. 2004; Wu and Giraldeau 2004).

We tested whether inter-individual differences in BMR were associated with differences in the use of high-variance (producer) and low-variance (scrounger) foraging tactics. Because BMR reflects the minimum energy requirement of an individual, we assume that individuals with high BMRs would have higher overall energy requirements than individuals with low BMRs (Daan et al. 1990; Ricklefs 1996). Therefore, because foraging trials were carried out early in the day, leaving foragers with much time to meet their energy requirements, we predicted that high BMR individuals would have a higher use of scrounger, the low-variance tactic, compared with low BMR individuals. We used captive-bred zebra finches (*Taeniopygia guttata*) because in zebra finches, BMR is both repeatable ($r^2 > 0.40$)

(Rønning et al. 2005) and heritable ($h^2 = 0.25$) (Rønning et al. 2007), and individual differences in BMR have been shown to be positively correlated with differences in daily energy expenditure (Vézina et al. 2006). Zebra finches are a widely used model system in behavioural studies (Zann 1996), including group foraging in a producer-scrounger game (Beauchamp 2006; Giraldeau et al. 1990).

BMR-related differences in foraging tactic use were predicted based on a dynamic variance-sensitive producer-scrounger model (Barta and Giraldeau 2000). However, phenotype-dependent tactic use could also generate BMR-related differences in the use of scrounger, if BMR is correlated with a phenotypic trait that influences tactic use. In order to test whether BMR-related differences in tactic use were due to variance-sensitive foraging, foraging trials were conducted under both high and low food abundance. Phenotype-dependent tactic use decisions may or may not be affected by food treatment. In contrast, variance-sensitive foragers should show higher use of the scrounger tactic with decreasing food abundance, if lower food abundance increases the probability of energetic shortfall (Barta and Giraldeau 2000). Therefore, if food abundance does not influence the use of the scrounger tactic, we can conclude that variance-sensitive foraging decisions do not underlie any BMR related differences in social foraging tactic use.

3.3 Methods

3.3.1 Study subjects

Zebra finches were maintained on a 12h:12h light:dark cycle (lights on from 6h00 to 18h00) at temperatures between 22 and 24°C in same-sex groups with ad libitum access to water at all times. Outside of experimental periods, the birds were housed together in cages (113 × 61 × 90 cm high) with ad libitum access to vitamin-supplemented commercial millet seed mixture.

3.3.2 BMR measurements

Between March and April 2007, we obtained measures of the BMR of 28 female zebra finches. We used females only to avoid confounding sex and BMR, as female zebra finches have higher BMRs than males (Rønning et al. 2005). Birds were taken from their holding aviaries and placed individually in the metabolic chambers at 1800 h in the evening (the start of their resting phase). Measurements of O_2 consumption were obtained over the 12 h resting phase, and the birds were removed from the chambers at 0600 h. We recorded the mass (to 0.01 g) and crop contents (number of seeds visible in the crop, (Zann and Straw 1984) of birds both immediately before being placed in the metabolic chambers and immediately after being removed from the metabolic chambers.

BMR was measured as O_2-consumption rates using a two-channel open flow respirometry system. H_20 and CO_2 were removed from influent air using Drierite ® and soda lime, and the air was then pumped through two metabolic chambers made from 900 mL metal cylinders with airtight lids. The chambers were maintained at 35 ± 5°C, which is within the thermoneutral zone of the zebra finch (Calder 1964). A constant air-flow rate into the chambers of 315 $mL \cdot min^{-1}$ was maintained using mass-flow controllers (Sierra Instruments, Monterey, CA, Side-track model 844). The O_2 concentration in effluent air streams (dried with Drierite®; Xenia, Ohio) was measured using two O_2 analyzers (Model FC-1, Sable Systems International; Henderson, NV). Two additional streams of dry and CO_2-free air were used to calibrate analysers at 20.95% O_2 (baseline). An automatic valve switched between streams, so that 10 min of baseline O_2 concentration were recorded for every 60 min measured in the chambers. We allowed one minute delay between switches in order to allow the system to wash out completely. Analog outputs from the O_2 analyzers and thermocouple inside chambers were fed to a computer via a 16-bit A/D converter card. Oxygen concentrations were recorded at 6 s intervals.

The rate of O_2 consumption (V_{O2}) was calculated using equation 3a from Koteja (1996) without absorbing CO_2 from effluent air prior to gas analysis as this minimizes error in the conversion of O_2 consumption to energy expenditure when the respiratory quotient is

unknown. Birds with seeds remaining in their crops in the morning were excluded (N = 3) from BMR estimates as they would not have attained post-absorptive status during the measurement period. We used ExpeData® (Sable Systems, LasVegas, Nevada) to select and calculate the lowest 10 min average V_{O2}, and this was used to represent the BMR. Body mass at the time of BMR measurement was used to calculate mass-specific BMR based on the assumption of linear body mass loss between the two successive mass measurements. In order to convert O_2 consumption to energy consumption, we used a respiratory quotient 0.8 (Koteja 1996).

3.3.3 Foraging trials

Of the 25 birds from which we obtained useable BMR measurements, one was not used during foraging trials because she began wing moult prior to experiments and had visibly reduced flying ability. We formed 4 flocks of 6 birds from the remaining 24 birds. Birds were categorized according to their BMRs: the 4 individuals with the highest BMRs were classified as 'high', the 4 individuals with the lowest BMRs were classified as 'low', and all other birds were classified as 'intermediate'. We randomly assigned birds to the four flocks with the constraint that each group contain 1 high and 1 low BMR bird. Prior to the start of experiments, one bird died, reducing the group size of one flock to 5. High and low BMR birds were given colour leg flags to allow for individual identification. In two flocks, high BMR individuals were banded with red colour flags, and low BMR individuals were banded with yellow colour flags. The colour scheme was reversed for the other two flocks.

Foraging trials took place in May and June 2007 in indoor aviaries (1.5 × 3.8 × 2.3 m high). Each aviary contained two large perches and a foraging grid placed on tables approximately 90 cm above the aviary floor, which allowed a seated observer to videotape the birds through a one-way mirror using a 8 mm color camcorder mounted on a tripod. The foraging grid was covered by a sheet of black plastic at all times except during the foraging trials. The perches were placed at the far end of the aviary so that birds could not see directly into the wells from the perches, but had to fly down to the foraging grid to search for food.

Birds were given 2 d to become familiar with the aviaries. Food was removed at 1800 h on the evening of the second day, and each evening thereafter (evenings 2 through 10). Trials commenced at 0830 h the following mornings (d 3 through d 14), 2.5 h after lights on. Thus, the birds were deprived of food for 14.5 h (12 h dark phase, plus 2.5 h the following morning) durations that were necessary given that zebra finches store seeds in their extensible crops for overnight use.

Foraging trials were conducted for 12 d (d 3 through d 14) 7 times per d at 1 h intervals. Each group was tested under 2 different food conditions: 'high' and 'low'. During the high food condition, 10 white millet seeds were placed in each of 20 randomly selected wells. During the low food condition, 10 white millet seeds were placed in 10 randomly selected wells for each trial. Following each trial, any remaining seeds or seed husks were removed from the grid before placing seeds in the new randomly selected wells. The grid was covered with a sheet of black plastic until the start of the next foraging trial, and birds typically rested on the perches during the inter-trial interval. The quantity of seeds available in the high and low food treatment were selected based on pre-trials which showed that the high food treatment resulted in an approximately neutral energy budget (average mass loss: 0.11 ± 0.06 g, $N = 6$), and the low food treatment resulted in a negative energy budget (average mass loss: 0.55 ± 0.06 g, $N = 6$).

In order to keep patch encounter rate similar between the two food conditions, the size of the foraging grids differed between food treatments. Although this would alter the density of birds on the foraging grids, neither variance-sensitive nor rate maximizing producer-scrounger models predict any effect of group density on the frequency of producer-scrounger foraging alternatives (Caraco and Giraldeau 1991; Vickery et al. 1991). Furthermore, unlike many other animals, zebra finches are very tolerant of conspecifics in close proximity to themselves, and do not show increased aggression with increased proximity of conspecifics (Caryl 1975).

During the high food treatment, the foraging grid consisted of 2 side by side plywood boards with a combined dimension of 2.0 by 1.2 m, in which there was a total of 198 wells.

In the low food condition, the foraging grid was made up of a single plywood board with dimensions of 1.0 by 1.2 m and a total of 99 wells. For both sets of foraging grids, wells were 1.3 cm in diameter, 0.8 cm deep, and spaced at 10 cm intervals. The order in which groups received the food treatments was randomized, with 2 groups receiving the high food treatment first, and 2 groups receiving the low food treatment first.

The first 3 d of foraging trials were used to train the birds on the seed distribution, and were not videotaped. The following 3 d of foraging trials were videotaped as the observer (KJM or SG) called out the location of individuals into the audio channel of the videotape recorder to facilitate the identification of the focal individual during the playbacks from which data were recorded. Videos were analyzed by a single observer (KJM). Following the final foraging trial for a given food abundance treatment, foraging grids were set up for the next food distribution (a grid was either removed or added to the aviary). Again, the first 3 d under the new food treatment served as training on the seed distribution, followed by 3 d of filming.

Body mass was measured before (0730 h) and after (1430 h) foraging trials each day by placing the bird in a paper bag and weighing it on a digital balance to 0.01 g. These mass recordings allowed us to assess mass change during the foraging trials.

3.3.4 Video analysis

Data were recorded from video playbacks of trials playing at 1/2 speed using Noldus Observer 5.0 Video Pro. Videos were observed in random sequence by KJM. Because colour bands were reversed for half of the groups (high BMR individuals were banded yellow and low BMR individuals banded red in 2 groups, and vice versa for the other 2 groups), the BMR status of the individual could not be inferred based on the colour of its leg bands when coding videos. Behavioural observations were made for both the high and low BMR bird in each group for each foraging trial. In ground feeding birds, individuals hop with the head oriented downwards when producing, and with the head oriented upwards while scrounging (Coolen et al. 2001). Therefore, we recorded the following behaviours: hop with head up

(imaginary line from the eyes through the nares is at or above horizontal), hop with head down (imaginary line is below the horizontal), produce patch (first to feed at patch), scrounge patch (feeding from a patch where ≥ 1 other bird is feeding), and off the grid. For the high food condition, half of the total available patches were discovered within approximately 60 s, whereas this occurred in the first 30 s for the low food condition. We therefore restricted behavioural observations to the first 60 s and the first 30 s of video playbacks for the 'high' and 'low' food abundance treatments respectively.

Producer-scrounger models predict relative use of the alternative foraging tactics (producer and scrounger) rather than absolute use of these tactics (Barta and Giraldeau 2000; Caraco 1981; Vickery et al. 1991). Therefore, for each trial we calculated proportion of hops with the head up (hops with head up / [hops with head up + hops with head down]) as an index of scrounger use. Because there were relatively few patch finding and patch joining events per individual within trials, we calculated the proportion of patches scrounged (no. patches scrounged / [no. patches produced + no. patches scrounged]) over all trials in a day.

3.3.5 Statistical analyses

All statistical analyses were carried out using R v.2.6.1 (R Development Core Team 2007). BMR values (in $J \cdot h^{-1} \cdot g^{-1}$) for the three categories of birds ('high', 'intermediate' and 'low') were compared using an ANOVA with 'BMR' as a fixed factor. Tukey HSD tests ('stats' library) were used to make comparisons between pairs of BMR levels.

The effective sample sizes in our experiments were small, with BMR and food abundance treatments being carried out in only 4 flocks. Furthermore, the large number of repeated observations made within flocks for a given set of conditions meant that there was significant pseudo-replication in our data set. Therefore, we used linear mixed-effects models (LMEs) to analyze both mass and behavioural data. LMEs provide estimates of the influence of fixed effects on the mean as well as the influence of random effects on the variance, thereby accounting for the non-independence of errors resulting from the repeated measures within flocks (Pinheiro and Bates 2000).

LMEs were constructed using the 'lme' function of the 'nlme' package in R. We calculated the change in mass during the foraging trials by subtracting the mass values recorded at 1430 h from mass values recorded at 0730 h. We tested whether mass change varied as a function of 'BMR' or 'food abundance' by including 'BMR' (high or low), 'food abundance' (high or low), and their interactions as fixed effects in the model, and flock, id within flock, and day within id within flock as random effects (~1| flock/id/day).

For analyses of behavioural data (proportion of hops with head up, and proportion of patches joined), BMR (high or low), food abundance (high or low), and their interaction were included as fixed effects in the models. Flock, id nested within flock, and trial nested within id nested within flock, were included as a random effects (random = ~1|flock/id/trial) in the model for proportion of hops with head up. Flock, id nested within flock, and day nested within id nested within flock, were included as a random effects (random = ~1|flock/id/day) in the model for proportion of patches joined.

Prior to analyses, proportion data were arcsine square root transformed to meet assumptions of normality and linearity (Zar 1999). We checked residuals for violations of model assumptions by visual inspection of residuals versus fitted values plots. Significance was set at $p < 0.05$ and non-significant interactions were removed from the models. Values presented are means ± s.e.

3.4 Results

3.4.1 BMR

Summary statistics for three representations of BMR ($mL \cdot O_2 \cdot hr^{-1}$, $mL \cdot O_2 \cdot hr^{-1} \cdot gr^{-1}$ and $J \cdot hr^{-1} \cdot gr^{-1}$) are provided in Table 3.1 in order to facilitate comparisons between the measures obtained in our study with those obtained in other studies. Energy consumption ($J \cdot h^{-1} \cdot g^{-1}$) differed significantly according to BMR category ($F_{2,20} = 5.09$, $p = 0.016$). High BMR birds differed significantly from both intermediate and low BMR birds (Tukey HSD, $q = 2.53$, $p <$

0.05), by 17 and 23%, respectively. BMR of intermediate and low BMR birds did not differ significantly from one another (Tukey HSD, $q = 2.53$, $p > 0.05$).

3.4.2 Daily variation in body mass

In the LME for change in body mass, the BMR × Food interaction was significant (Table 3.2). High BMR birds lost mass throughout the foraging trials during the low food abundance treatment, but gained mass during the high food abundance treatment. Low BMR birds lost mass throughout foraging trials during the low food abundance treatment, and maintained stable mass during the high food abundance treatment (Figure 3.2).

3.4.3 Foraging behaviour

The effect of BMR on the proportion of hops made with the head up did not differ according to food treatment (BMR × Food: $p > 0.50$). However, the proportion of hops made with the head up was significantly affected by 'BMR' ($F_{1,3} = 12.03$, $p = 0.040$, Table 3.2, Figure 3.3). High BMR birds had a higher use of the scrounger tactic compared with low BMR birds. There was no effect of 'Food' on the proportion of hops made with the head oriented upwards ($F_{1,167} = 2.70$, $p = 0.10$, Table 3.2).

The effect of BMR on the proportion of patches joined did not vary according to food treatment (BMR × Food: $p > 0.50$). Although individuals with higher BMRs tended to join a greater proportion of patches than low BMR individuals, this effect just failed to reach conventional levels of statistical significance ($F_{1,3} = 7.92$, $p = 0.067$, Table 3.2, Figure 3.4). Again, food abundance treatment did not affect the proportion of patches joined ($F_{1,39} = 1.35$, $p = 0.25$, Table 3.2).

3.5 Discussion

Dynamic variance-sensitive producer-scrounger foraging model predicts that increasing an individual's expectation of energetic shortfall should result in an increased use

of the variance-averse tactic, scrounger, early in the foraging period (Barta and Giraldeau 2000). We tested for an effect of BMR on scrounging behaviour. We assumed that higher BMR equates with greater expectation of energy shortfall, all else being equal, because higher BMR is associated with higher daily energy requirements (Vézina et al. 2006). Individuals with high BMRs did have a greater use of the scrounger tactic compared with individuals with low BMRs. These results match qualitative predictions from Barta and Giraldeau's (2000) dynamic variance-sensitive social foraging model. However, birds did not adjust their use of producer and scrounger tactics when foraging at two different levels of food abundance, as would also have been expected in a dynamic variance-sensitive foraging game (Barta and Giraldeau 2000) and so variance-sensitive foraging cannot account for the birds' behaviour.

We observed a significant effect of BMR on scrounger investment but we did not detect a significant effect of BMR on the proportion of patches joined. Nonetheless, the direction of the trends observed in the proportion of patches joined with respect to BMR level are the same as for proportion of hops with the head up. High BMR birds tended to join a greater proportion of patches than low BMR birds, with the exception of one low BMR individual which did not conform to this pattern in the low food treatment. Removal of this individual from the analysis resulted in a significant effect of BMR on the proportion of patches joined in both high ($F_{1,2} = 34.63$, $p = 0.03$) and low ($F_{1,2} = 26.12$, $p = 0.04$) food treatments. The finding that high BMR individuals had greater use of the scrounger foraging tactic (proportion of hops with head up) is similar to those reported for house sparrows (*Passer domesticus*), which increased their use of scrounger when their energetic requirement was experimentally manipulated using fans to increase their overnight energy loss (Lendvai et al. 2004; Lendvai et al. 2006).

The patterns of mass change across food treatments indicate that the probability of energetic shortfall was greater in the low food abundance treatment. However, individuals did not adjust their use of the scrounger tactic according to food abundance. Thus, given that the focal individuals were insensitive to the large differences in the probability of energetic shortfall between the two food abundance treatments, variance-sensitivity is not likely to

underlie the observed BMR-related differences in tactic use. However, the relationship between foraging behaviour and BMR observed in this study is robust, and provides the first demonstration that variation in BMR within a species is associated with differences in foraging behaviour.

The mechanism underlying the relationship between foraging behaviour and BMR remains to be examined. However, we suggest that the use of producer and scrounger foraging tactics is phenotype-dependent, and the relationship between BMR and tactic use may arise because BMR is correlated with another phenotypic character that influences tactic use decisions. Higher BMR may correlate with higher dominance rank (Buchanan et al. 2001), and dominance rank has been suggested as a possible factor mediating producer-scrounger foraging decisions (Barta and Giraldeau 1998; Giraldeau and Beauchamp 1999). However, in zebra finches, BMR is repeatable over periods of years (Rønning et al. 2005), while dominance rank is unstable over periods of days (Caryl 1975; Evans 1970). Furthermore, two previous studies have failed to find any effect of dominance rank on producer-scrounger tactic use in this species (Beauchamp 2006; Giraldeau et al. 1990). We therefore suggest that it is unlikely that BMR related differences in producer-scrounger foraging tactic use observed in this study reflect dominance-mediated foraging decisions.

An alternative possibility is that differences in BMR reflect differences in body composition (Daan et al. 1990; Scott et al. 1992), which in turn affect individuals' ability to use producer and scrounger alternatives. Hopping rates are greater when employing the scrounger tactic compared with the producer tactic (Wu and Giraldeau 2004). Rapid movement while scrounging may be beneficial, because the sooner a scrounger arrives at the patch, the more food there will be remaining for it to share in eating. Individuals that are able to power more rapid movement should receive greater payoffs when playing the scrounger tactic compared with individuals that are not able to do so. Rapid movement would presumably require more muscle, and muscle is a highly metabolically active tissue (Scott et al. 1992). Thus, relatively greater amounts of muscle for a given body mass could at once increase an individual's mass specific BMR and their ability to play scrounger. Differences in muscle mass have also been suggested to underlie inter-specific differences in BMR and

foraging behaviour in two orders of birds. Among both Caprimulgiformes (McNab and Bonaccorso 1995) and Falconiformes (Wasser 1986), species using foraging modes that require greater muscle power also have higher BMRs. For example, birds of prey that use powered flight to catch prey have higher BMRs than those which hunt primarily by soaring (Wasser 1986).

Phenotype-dependent tactic use decisions would account for the surprising patterns of mass change across foraging trials. Both high and low BMR birds showed similar levels of mass loss during the low food abundance treatment. However, high BMR birds gained mass in the high food abundance treatment while low BMR birds maintained stable mass. This indicates that high BMR individuals received greater payoffs than low BMR birds in the high food abundance treatment. If the payoff to producer and scrounger foraging alternatives were strictly frequency-dependent, all individuals should receive equal payoffs at equilibrium (Vickery et al. 1991). However, if the payoffs to producer and scrounger are both frequency- and phenotype-dependent, then payoffs should be equal within phenotypes, but not necessarily between phenotypes (Repka and Gross 1995).

Earlier studies have demonstrated that inter-specific differences in BMR correlate with differences in foraging behaviour (McNab 2002). However, this study is the first to report that variation in BMR within a species is associated with differences in foraging behaviour. Although the reason for BMR-related differences in scrounger tactic use is unresolved, the relationship between BMR and scrounger tactic use does not seem to be driven by variance-sensitive foraging decisions. The results are consistent with the notion that allocation decisions to producer-scrounger tactics are phenotype-dependent. Other phenotypic constraints on tactic use have been identified for producer-scrounger foraging, including levels of energy reserves (Lendvai et al. 2006; Wu and Giraldeau 2004), dominance status (Lendvai et al. 2006; Liker and Barta 2002), foraging efficiency (Beauchamp 2006), and individual vulnerability to predation (Mathot and Giraldeau 2008). Our results suggest that an aspect of phenotype, which covaries with BMR, may also be influencing tactic use decisions in female zebra finches.

3.6 Acknowledgements

These experiments conform to guidelines of the Canadian Council for Animal Care and were approved by the University Animal Care Committee (0307-571-0208). We thank Joe Nocera and Julien Martin for statistical advice, and three anonymous referees for constructive comments. This research was supported by an NSERC Discovery Grant to L.-A.G. KJM was financially supported by a Natural Sciences and Engineering Research Council (Canada) scholarship.

Table 3.1: Mass-dependent and mass-specific basal metabolic rate (BMR) expressed as oxygen consumption and energy expenditure of female zebra finches according to their classification into low, intermediate, and high categories. Values presented are means ± 1 s.e. Sample sizes are indicated in parentheses.

	Low BMR (4)	Intermediate BMR (15)	High BMR (4)	Overall (23)
$mL \cdot O_2 \cdot hr^{-1}$	36.79 ± 1.46	39.97 ± 0.75	49.15 ± 1.46	41.01 ± 1.02
$mL \cdot O_2 \cdot hr^{-1} \cdot g^{-1}$	2.69 ± 0.19	2.89 ± 0.10	3.49 ± 0.19	2.96 ± 0.09
$J \cdot hr^{-1} \cdot g^{-1}$	54.21 ± 3.83	58.18 ± 1.98	70.21 ± 3.83	59.58 ± 1.87

Table 3.2: Linear mixed-effects model for a) daily patterns of mass change, b) proportion of hops with the head up, and c) proportion of patches joined in female zebra finches. The models include the following random effects: flock, id nested within flock, and day (or trial) nested within id nested within flock.

Source of variation	num DF	den DF	F-value	p-value
a) Daily patterns of mass change				
BMR	1	3	25.78	0.015
Food	1	22	194.75	< 0.0001
BMR × Food	1	22	17.41	0.0004
b) Arcsine square root (proportion of hops with head up)				
BMR	1	3	12.03	0.04
Food	1	167	2.70	0.10
c) Arcsine square root (proportion of patches joined)				
BMR	1	3	7.92	0.067
Food	1	39	1.35	0.25

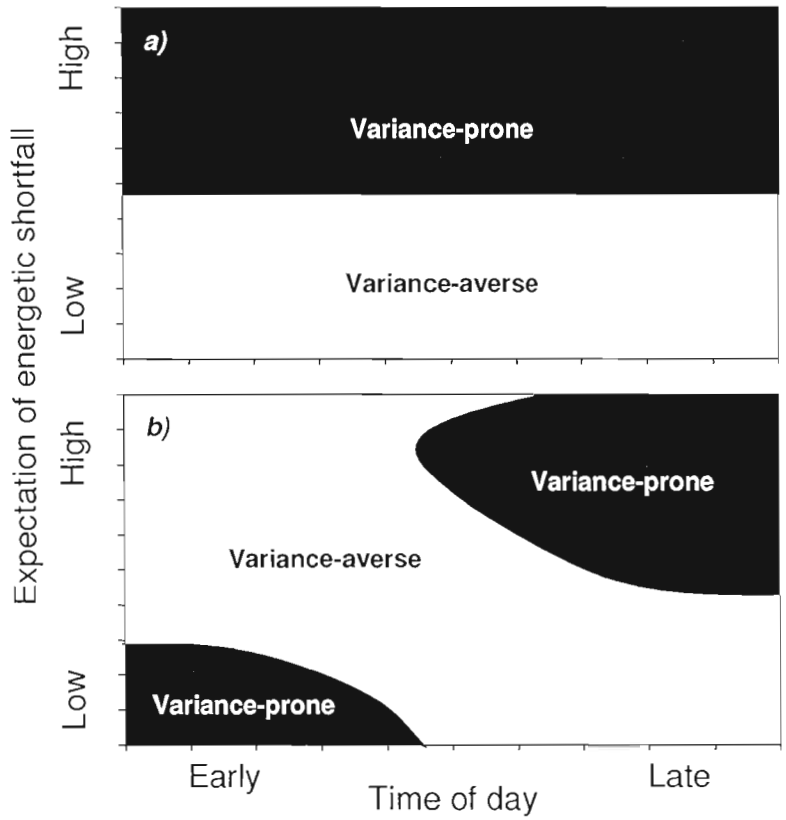

Figure 3.1: Schematic representations of predictions from a) static, and b) dynamic variance-sensitive foraging models with respect to an individual's expectation of energetic shortfall and the time of day. Figure b) is adapted from Barta and Giraldeau 2000. Note that predictions for variance-prone or variance-averse behaviour do not imply absolute preferences in producer-scrounger foraging.

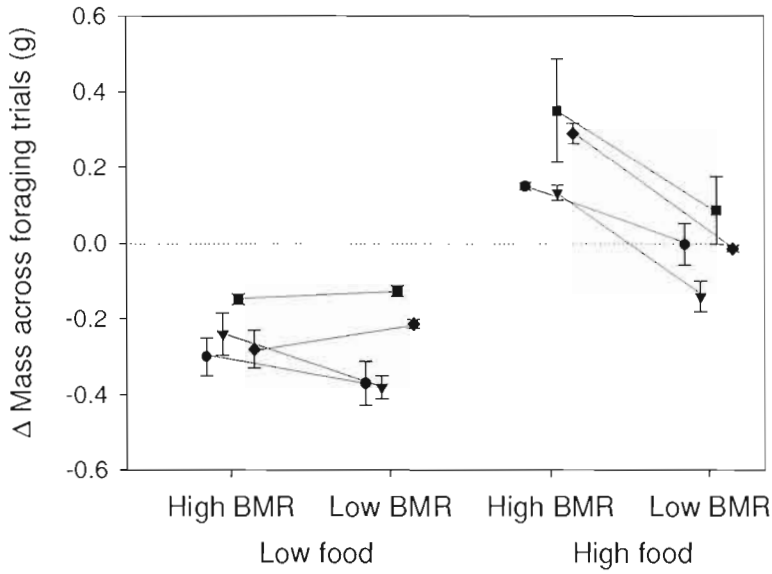

Figure 3.2: Change in mass (g) during foraging trials (from 0730 h to 1415 h) as a function of food abundance treatment and basal metabolic rate (BMR) in female zebra finches. Dashed line indicates no mass change. Solid lines connect high and low BMR individuals from the same flock under the same food conditions. Each symbol denotes a different flock. Values presented are means ± 1 s.e.

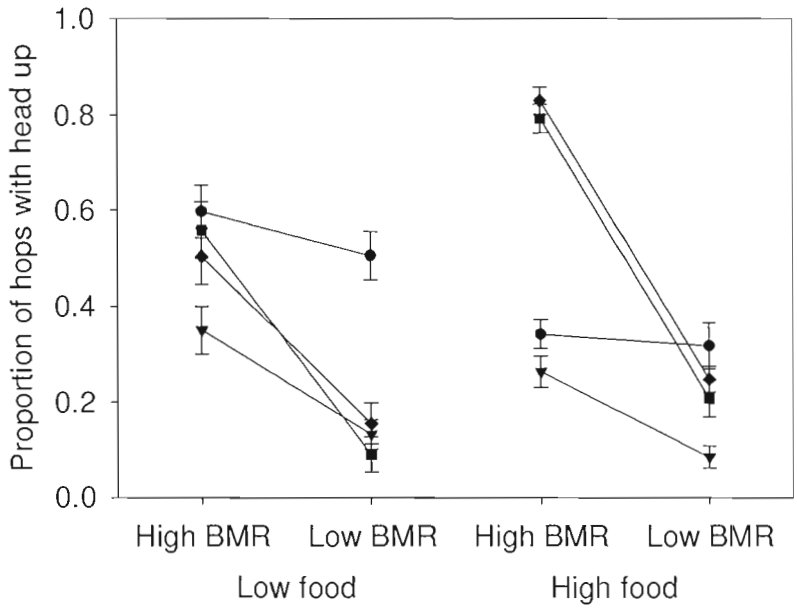

Figure 3.3: Investment in the scrounger tactic (proportion of hops made with the head oriented upwards) according to basal metabolic rate (BMR) and food abundance in female zebra finches. Each symbol denotes a different flock. Lines connect high and low BMR individuals from the same flock under the same food conditions. Note that the data presented are untransformed, while proportion data were arcsine square root transformed for statistical analyses. Values presented are means ± 1 s.e.

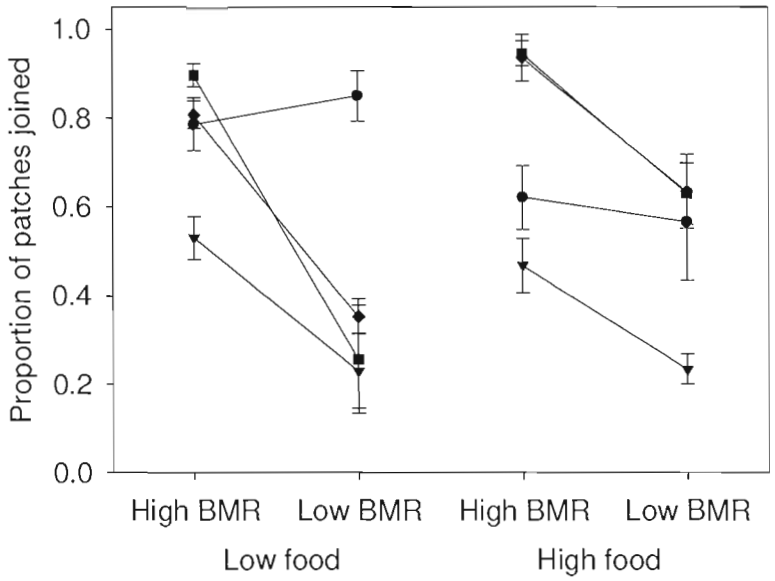

Figure 3.4: Proportion of patches joined according to basal metabolic rate (BMR) and food abundance in female zebra finches. Each symbol denotes a different flock. Lines connect high and low BMR individuals from the same flock under the same food conditions. Note that the data presented are untransformed, while proportion data were arcsine square root transformed for statistical analyses. Values presented are means ± 1 s.e.

PREAMBLE

In the previous two chapters, we provide evidence that producer-scrounger tactic use decisions in zebra finches are condition-dependent. We identified two state variables (vulnerability to predation and basal metabolic rate, BMR) that influence tactic use. Because various aspects of individual state are heritable, observed tactic use under the conditional strategy may also be heritable. In this chapter, we look for evidence of heritability in social foraging tactic use in the zebra finch by testing for family-related differences in tactic use.

This chapter is presented in the form of an article that has been submitted to Behavioral Ecology and Sociobiology (Manuscript number: BES-10-0037, submitted 17 January 2010). Kimberley Mathot was responsible developing the research question, the design and implementation of the experiment, data analysis and writing the manuscript. Luc-Alain Giraldeau provided guidance throughout, and provided comments on the manuscript.

CHAPTER 4

FAMILY-RELATED DIFFERENCES IN BODY CONDITION AND SOCIAL FORAGING TACTIC USE IN THE ZEBRA FINCH (*TAENIOPYGIA GUTTATA*)

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4.1 Abstract

When animals forage in groups, they can search for food themselves (producer tactic), or they can search for opportunities to exploit the food discoveries of others' (scrounger tactic). Group-level use of these alternative tactics is influenced by environmental conditions including group size and food distribution, and individual tactic use can be influenced by several measures of individual state, including body condition. Because body condition has been shown to be heritable for various species, observed tactic use may also be heritable. We looked for evidence of heritability in social foraging tactic use in the zebra finch (*Taeniopygia guttata*) by testing whether: 1) natural variation in body condition correlates with tactic use, 2) there are family-related differences in body condition, and 3) there are family-related differences in observed tactic use. Tactic use in the zebra finch was significantly related to body condition; individuals with lower body condition scores had a significantly higher use of the scrounger tactic as predicted from variance-sensitive producer scrounger models. Body condition scores differed significantly between families, suggesting that this aspect of individual state may have a heritable component. Finally, we recorded significant family-related differences in the use of producer and scrounger alternatives. These results are consistent with heritability in observed tactic use resulting from an inheritance of individual state, in this case body condition, which itself influences tactic use. Understanding how and why individuals differ in their use of alternative tactics is fundamental as it may provide important insights into inter-individual variation in fitness.

4.2 Introduction

Social foraging is one of the best-studied examples where individuals use alternative tactics (Giraldeau and Caraco 2000). When animals forage in groups, individuals can search for food themselves (producer tactic) or they can search for other individuals that have located food in order to exploit their discovery (scrounger tactic) (Giraldeau and Caraco 2000). Both tactics are maintained in groups via frequency dependence because each tactic does better relative to the other when it is rare (Giraldeau and Caraco 2000; Mottley and Giraldeau 2000; Vickery et al. 1991). Consequently, at some intermediate frequency, the payoff to both tactics is equal. This point is known as the stable equilibrium frequency (SEF) (Mottley and Giraldeau 2000).

The SEF of tactic use within groups is influenced by several conditions. Increasing group size and/or increasing food patch size favour a higher use of the scrounger tactic (Coolen 2002; Coolen and Giraldeau 2003; Vickery et al. 1991). Several studies have noted that when the SEF changes, individuals retain consistent differences in their use of producer-scrounger alternatives (Beauchamp 2001; Koops and Giraldeau 1996; Morand-Ferron et al. 2007). Individuals with a relatively low use of scrounger in condition A continue to have a low use of scrounger relative to their group mates in condition B, and vice versa. This suggests that tactic use may also depend on an individual's phenotype. In fact, several individual state variables have been identified that influence individual tactic use, including levels of energy reserves (Lendvai et al. 2004; Lendvai et al. 2006; Wu and Giraldeau 2004), basal metabolic rate (Mathot et al. 2009), vulnerability to predation (Barta et al. 2004; Mathot and Giraldeau 2008), dominance (Lendvai et al. 2006; Liker and Barta 2002), and foraging efficiency (Beauchamp 2006). Given that some of the measures of individual state known to influence tactic use may also be heritable, including body condition (Blanckenhorn and Hosken 2003; Gosler and Harper 2000; Merilä et al. 2001; Phillips and Furness 1998), basal metabolic rate (Rønning et al. 2007), and dominance status (Boag and Alway 1981), producer-scrounger foraging provides a tractable system for investigating potential for heritability of condition-dependent tactic use (Gross and Repka 1998a; Gross and Repka 1998b; Hazel et al. 1990).

Here, we test whether natural variation in body condition, as indicated from the residuals of a regression of body mass against tarsus length (Pärt 1990), are correlated with tactic use decisions in the zebra finch (*Taeniopygia guttata*). Previous studies have shown that individuals increase their investment in the scrounger tactic following an experimental reduction in energy reserves (Lendvai et al. 2004; Lendvai et al. 2006), as predicted by a variance-sensitive producer-scrounger model (Barta and Giraldeau 2000). However, it is unclear whether natural variation in body condition is sufficient to generate individual differences in tactic use. We also test whether there are family-related differences in body condition, because body condition has been reported to be heritable in other systems (Blanckenhorn and Hosken 2003; Gosler and Harper 2000; Merilä et al. 2001; Phillips and Furness 1998). If producer-scrounger tactic use decisions are influenced body-condition, and body-condition is heritable, then observed tactic use may also show heritable variation (Gross and Repka 1998a; Gross and Repka 1998b; Hazel et al. 1990).

To date, empirical demonstrations of inheritance of tactic use under a conditional strategy are scarce (but see Garant et al. 2003; Thériault et al. 2007), and further investigations into how and why individuals differ in their use of alternative tactics is warranted. If tactic use decisions are influenced by individual state variables which are inherited, it may provide important insights into inter-individual variation in fitness.

4.3 Methods

4.3.1 Study subjects and aviaries

Breeding was carried out between January and June 2008 using outbred domesticated zebra finches obtained from a commercial supplier. Adult zebra finches were paired randomly and each pair was housed in an individual cage (57 × 29 × 42 cm) to allow unambiguous parentage assignment. Each cage contained two perches, one reed nest and nesting materials. Birds were maintained on a 12h:12h light:dark cyle (lights on from 6h00 to 18h00) at 22 to 24°C. During breeding and outside of experimental periods, birds had ad

libitum access to water, vitamin-supplemented commercial millet seed mixture, cuttlefish bone, and crushed oyster shells. Additionally, birds were provided with fresh fruits and vegetables three times per week, and a protein supplement once per week.

Chicks were removed from their natal cage at independence (mean ± SE = 42.3 ± 0.7 d after hatching), and housed in single sex groups with non-family members for a period of 1.5 to 5 months prior to experiments. Full-siblings were not always produced from the same clutch, consequently, 'age' and 'family id' were not confounded in this study. We formed 5 mixed-sex flocks of 5 birds each. Each flock was comprised entirely of non-siblings, and 6 families were replicated between 2 and 5 times (by individuals from that family being present in different flocks). Three individuals were used which had no other full-sibling in any other flock, and these individuals were excluded from analyses which included 'Family' as a fixed effect. Within each group, individuals were provided with a unique leg flag colour. Birds were not used in experiments until they reached at least 90 days of age, to ensure that they had completed development (Zann 1996).

4.3.2 Experimental procedure

During experiments, flocks were placed in indoor aviaries (1.5 × 3.8 × 2.3 m high). Immediately before introducing flocks into the aviaries, we measured tarsus length and body mass of each individual to obtain an index of body condition (see below). Body mass measurements for all individuals were taken at similar times, between 13h00 and 14h00, to control for diurnal variation in body mass.

Each aviary contained two large perches and a foraging grid. The foraging grid consisted of two plywood boards, positioned side by side so that their combined dimensions were 2.2 by 1.1 m, in which a total of 200 wells 1.5 cm in diameter, 0.8 cm deep, and spaced at 10 cm intervals were drilled. Foraging grids were placed on tables approximately 90 cm above the aviary floor, which allowed a seated observer to videotape the birds through a one-way mirror using a digital video camera mounted on a tripod. The foraging grid was covered by a sheet of black opaque plastic at all times except during the foraging trials. The perches

were placed at the far end of the aviary away from the grids preventing perching birds from seeing directly into the wells.

Birds were given 2 d to become familiar with the aviaries. Food was removed at 18h00 on the evening of the second day and each evening thereafter (evenings 2 through 9). Trials commenced at 8h00 the following mornings (days 3 through 10). Thus, the birds were deprived of food during the 12h dark phase, plus an additional 2h after lights on, durations that were necessary given that they store seeds in their extensible crops for overnight use.

Foraging trials were conducted for 8 d (days 3 through 10), 5 times per d at 1 h intervals. Before each foraging trial, 10 millet seeds were placed in each of 20 randomly selected wells. Trials typically lasted circa 5 min, after which time, all the patches on the foraging grid had been exploited and the birds returned to the perches. Birds were given ad libitum access to food following the final foraging trial each day (from 12h40 to 18h00).

Each foraging trial was videotaped as the observer called out the location of individuals into the audio channel of the camera to facilitate the identification of the individuals during the playbacks from which data were recorded.

4.3.3 Video analysis

Each video file of foraging trials was assigned a coded name in order to allow a single observer (KJM) to score the videos while remaining blind to the family identity and body condition score of the individual being observed. Videos were scored in random order using Noldus Observer 5.0 Video Pro. We scored the finding and joining events of each flock member up until the 10^{th} patch discovery of the flock. This procedure was adopted to standardize the effect of patch depletion between trials, by controlling for variation in the time required to locate patches either between flocks or across trials. A finding event was defined as an event where the focal individual was the first to encounter and feed at a patch and can be seen as the outcome of investing in the producer tactic. A joining event was defined as an event where the focal individual moved towards a patch with at least one other

bird already there and can be seen as the outcome of investing in the scrounger tactic. Because there were few finding and joining events for a given individual per trial (finding events: range 0 to 7 per individual per trial; joining events: range 0 to 10 per individual per trial), we summed the total number of finding and joining events in a given day to calculate the daily proportion of patches scrounged for each individual (N joining / (N finding + N joining)).

4.3.4.Statistical analyses

All statistical analyses were carried out using R v.2.8.0 (R Development Core Team 2007). We tested whether individual differences in the proportion of patches scrounged related to body condition. Body condition was estimated as the residual from a linear regression of body mass on tarsus length, and each unit of body condition corresponds to a 1g deviation from the allometrically expected mass (Pärt 1990). We constructed a linear mixed effects (LME) model with the proportion of patches scrounged as the dependent variable, following arcsine square root transformation to normalize the data (Zar 1999). 'Body condition', 'Day', and their interaction were included as fixed effects, and 'flock' as well as 'individual' nested within flock (~1|flock/individual) were included as random effects to account for the non-independence of repeated measures on the same individuals, and of individuals tested in the same flock (Pinheiro and Bates 2000). We also tested whether there were significant family related differences in body condition using an ANOVA with 'Family' as a fixed effect ('aov' function).

Finally, we tested whether family identity was a significant predictor of the use of the scrounger tactic, as indicated by the proportion of patches joined, using LME models ('lme' function from the 'nlme' library, Pinheiro et al. 2008). The proportion of patches joined was used as the dependent variable in the analyses, following an arcsine square root transformation to normalize the data. 'Family', 'Day' (1 through 8), and their interaction were included as fixed effects. 'Day' was included in the model to account for possible changes in the proportion of patches scrounged as individuals gained experience with foraging conditions such as the distribution of food patches. The 'Family × Day' interaction

was included to test whether families differed in their adjustment of scrounger use across days. 'Flock', and 'individual' nested within 'flock' were included as random effects (~1|flock/individual).

Tests not involving 'Family' as a fixed effect were carried out using data from all 25 individuals over 8 observation days. Tests involving 'Family' as a fixed effect were carried out using data from 22 individuals over 8 observation days, in order to exclude the 3 individuals that had no full-siblings present in other flocks.

4.4 Results

We recorded body condition indices ranging from -3.7 to 4, and body condition was significantly related to the proportion of patches scrounged (Table 4.1, Figure 4.1). Individuals with high body condition indices had a lower proportion of joining than individuals with low body condition indices. Although the proportion of patches scrounged decreased across days, the decrease was less for individuals with high body condition indices (LME: Body condition × Day interaction, $F_{1,173} = 4.54$, $p = 0.03$, see Table 4.1). Body condition indices differed significantly between families (ANOVA: $F_{1,5} = 7.51$, $p < 0.001$; Figure 4.2). We also recorded significant family-related differences in tactic use (Figure 4.3). Again, the proportion of patches scrounged declined across days, however, families showed significant differences in the extent of this decline (LME: Family × Day interaction, $F_{5,148} = 2.56$, $p = 0.03$; see Table 4.2).

4.5 Discussion

We found that natural variation in body condition was related to differences in the use of producer-scrounger alternatives. Individuals of higher body condition scrounged less than individuals of low body condition, similar to findings from earlier studies on house sparrows (*Passer domesticus*) (Lendvai et al. 2004; Lendvai et al. 2006). We also found significant family-related differences in body condition, suggesting that this measure of individual state may be heritable in the zebra finch, as has been reported in other species

(Blanckenhorn and Hosken 2003; Gosler and Harper 2000; Merilä et al. 2001; Phillips and Furness 1998). Finally, we recorded family-related differences in tactic use. Thus, taken together, these results are consistent with heritability in observed tactic use resulting from an inheritance of individual state, in this case body condition, which itself influences tactic use.

We used the residuals from a regression of body mass against tarsus length as an index of body condition in this study. A potential criticism of this body condition index is that residual body mass values do not identify the specific body components (ie. fat versus muscle) contributing to the residual variation (Gosler and Harper 2000; Green 2001). However, studies have shown that residuals of body mass against body size reflect differences in the amounts of both muscle and fat, thus positive residuals do reflect higher fat reserves and vice versa for negative residuals (Schulte-Hostedde et al. 2005 and references therein). Furthermore, there is no *a priori* reason to expect that higher amounts of muscle relative to body size should result in lower use of the scrounger tactic, while variation in energy reserves are predicted to influence tactic use (Barta and Giraldeau 2000; Dall and Johnstone 2002).

Consistent with our interpretation that the body condition index used here reflects variation in energy reserves, we observed that individuals with lower body condition scores scrounged more than individuals with higher body condition scores. This result can be understood in the context of variance-sensitive foraging behaviour, with lower energy reserves prompting individuals to adopt the tactic that yields less variable rewards, scrounger (Barta and Giraldeau 2000). Although similar results were reported in earlier studies which experimentally manipulated the energy reserves of house sparrows (Lendvai et al. 2004; Lendvai et al. 2006), to our knowledge, this is the first study to show that natural variation in body condition is associated with differences in social foraging tactic use.

Tactic use was also strongly influenced by 'Day'. As individuals gained more experience with the foraging grid, they decreased their use of scrounger. This may be due to an increase in foraging efficiency resulting from increased familiarity with the distribution of food. Similar results were reported in another study on zebra finches; where individuals with

prior experience with the foraging conditions had a higher use of producer than those with no prior experience (Beauchamp 2000a). However, we also observed a significant 'Body condition × Day' interaction, as well as 'Family × Day' interaction on the frequency of scrounging, indicating that individuals differ in the magnitude of their response to increased experience with the foraging conditions.

Body condition differed significantly between families, suggesting the possibility that such differences are heritable. Heritability of body condition has been reported elsewhere (Gosler and Harper 2000 and references therein), however, these studies focused on animals under natural conditions. As such, heritable variation in body condition has been interpreted as potentially reflecting heritable variation in the ability to compete for resources (Gosler and Harper 2000). In this study, the differences in body condition reported were measured following an extended period of ad libitum feeding (2 to 5 months post-fledging), and therefore do not reflect differences in access to food. Given that body condition indices differed significantly between families, this suggests the intriguing possibility that there is heritable variation in the level of energy reserves that individuals maintain. Maintaining energy reserves can be seen as a form of insurance to buffer against uncertainty in future feeding opportunities (Dall and Johnstone 2002). Thus, our finding of family-related differences in the propensity to maintain energy reserves may reflect heritable differences in how animals manage uncertainty.

We recorded significant family-related differences in a trait (body condition) that influences tactic use (producing vs. scrounging) as well as family-related differences in tactic use. The study design employed here, comparisons between full-siblings, does not allow us to disentangle the cause of family-related differences in body condition and tactic use. Although our results are consistent with heritability of tactic use, full-siblings in this study shared common parental, environmental, and genetic effects, each of which may have contributed to similarities in body condition, and hence tactic use, between siblings. Further studies will be needed to separate these effects.

Regardless of the mechanism(s) underlying the family-related effects in body condition and tactic use, several important inferences can be drawn from our findings. Although individuals are able to adjust their investment in producer-scrounger alternatives according to the prevailing conditions (Coolen 2002; Morand-Ferron et al. 2007; Mottley and Giraldeau 2000), individual differences in tactic use resulting from a conditional strategy indicate that individual flexibility in tactic use may be limited. Consequently, the frequency of alternative tactics in a group may vary depending on the specific individuals making up the group (Repka and Gross 1995). Since the payoffs to producer and scrounger alternatives are frequency-dependent (Giraldeau and Caraco 2000; Mottley and Giraldeau 2000), differences in the frequency of tactics between groups would result in differences in intake rates between groups. While it has previously been suggested that individuals should be able to gauge the condition of others in order to adjust their own behaviour (Lendvai et al. 2004), our result suggest that individuals might gauge the condition or tactic use of others in order to join groups of individuals whose use of producer and scrounger tactics best complement their own behavioural profile.

The potential for heritability in observed tactic use under a conditional strategy has been recognized for some time (Gross and Repka 1998a; Gross and Repka 1998b; Hazel et al. 1990), but there have been few demonstrations to date. Studies which have found evidence for heritability in tactic use involved tactics which, once adopted by an individual, become fixed (Garant et al. 2003; Thériault et al. 2007). Our results differ in this sense, as they show that genetic and/or shared parental and environmental effects early in life can generate consistent individual differences in a flexible behavioural trait.

4.6 Acknowledgments

These experiments conform to guidelines of the Canadian Council for Animal Care and were approved by the University Animal Care Committee (0108-601-0109). We are grateful to Neeltje Boogert for help with the breeding of the zebra finches, Jan Wijmenga for constructing the foraging grids, Neeltje Boogert and Jan Wijmenga for comments on an earlier version of the MS, and Denis Réale and members of the Giraldeau lab for helpful

discussions. KJM was supported by an NSERC graduate scholarship, an NSERC Discovery grant to L.-A.G, and a Bourse d'Excellence de l'UQAM.

Table 4.1: LME results for tactic use as a function of body condition and day. Tactic use (the proportion of joining events for each individual summed over the entire day), was arcsine square root transformed prior to analysis.

	DF	F	p
Source of variation			
Body condition	19	4.00	0.06
Day	173	38.57	<0.0001
Body condition × Day	173	4.54	0.034

Table 4.2: LME results for the proportion of joining as a function of 'Day', 'Family' and their interaction. Proportion of joining was calculated for each individual over 5 trials in a given day, and was arcsine square root transformed prior to analyses to normalize the data.

	DF	**F**	**p**
Source of variation			
Day	148	28.27	< 0.0001
Family	12	3.41	0.04
Family × Day	148	2.56	0.03

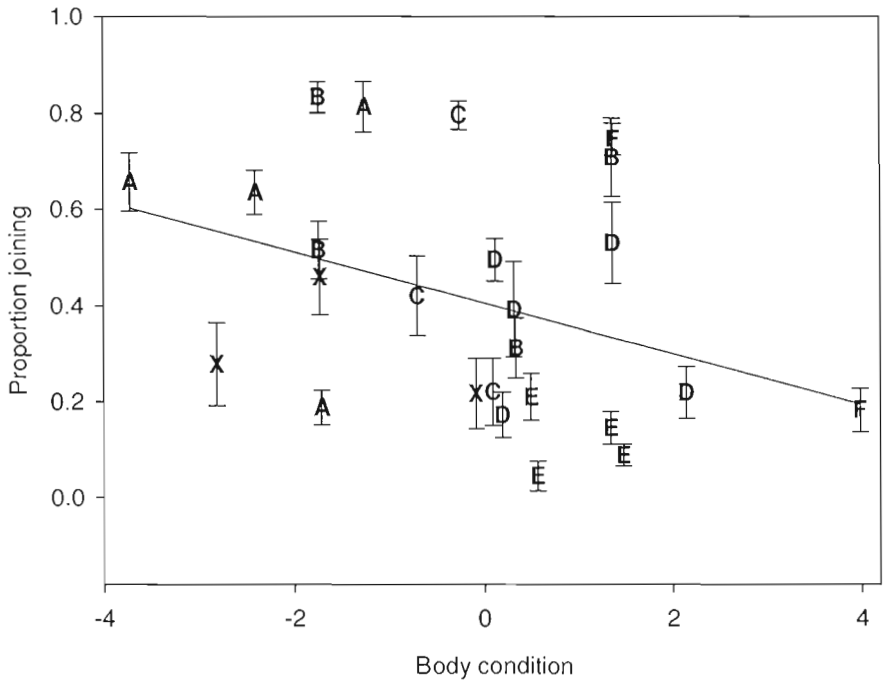

Figure 4.1: The proportion of patches joined (an index of investment in the scrounger tactic) as a function of 'Body condition'. Values presented are means ± 1 s.e. Note that while the model calculations were performed on arcsine square root transformed proportions, untransformed proportions are illustrated in the figure. Individuals from the same families are indicated by the same letter. X's denote the 3 individuals with no full-siblings.

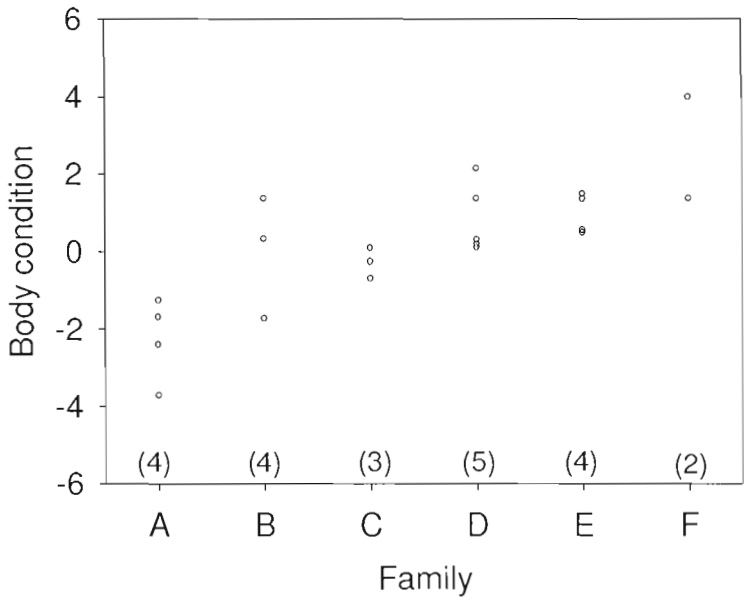

Figure 4.2: Family related differences in body condition. Body condition was estimated as the deviation from a linear regression of body mass (g) on tarsus length (mm). Thus, each unit represents 1 g deviation from the allometrically expected mass. Families were ordered on the x-axis from lowest to highest mean body condition. The number of individuals per family is indicated in parentheses above the x-axis.

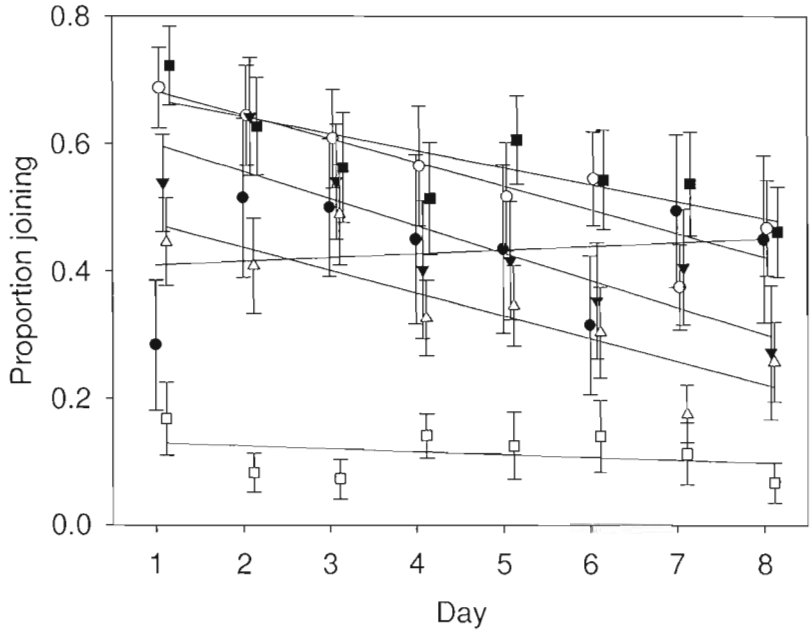

Figure 4.3: The proportion of patches joined (an index of investment in the scrounger tactic) as a function of 'Family' and 'Day'. Each line denotes a separate family, and is calculated from the linear mixed effects model estimates. Note that while the model calculations were performed on arcsine square root transformed proportions, untransformed proportions are illustrated in the figure. Points for different families on the same day are offset from one another for clarity.

PREAMBLE

In the previous chapter, we report family-related differences in producer-scrounger tactic use. When tested in different flocks, individuals from the same family group (ie. full-siblings) were more similar in their tactic use than expected by chance. In this chapter, we consider how foraging in family-groups versus non-family groups influences group level use of producer-scrounger tactics. We extend an existing rate-maximizing producer-scrounger model to incorporate inclusive fitness effects when foraging with relatives versus non-relatives, and test the model predictions empirically.

This chapter is presented in the form of an article which has been provisionally accepted for publication in Behavioral Ecology (Manuscript number 2009-0525-R1, accepted 7 April 2010). Kimberley Mathot was responsible developing the model, the design and implementation of the experiment, data analysis and writing the manuscript. Luc-Alain Giraldeau provided guidance throughout and read and commented on the manuscript prior to submission.

CHAPTER 5

WITHIN-GROUP RELATEDNESS CAN LEAD TO HIGHER LEVELS OF EXPLOITATION: A MODEL AND EMPIRICAL TEST IN SOCIALLY FORAGING ZEBRA FINCHES (*TAENIOPYGIA GUTTATA*)

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5.1 Abstract

When animals live in groups, individuals can invest in resources themselves, or exploit the investments of other group members. Grouping with kin may reduce the frequency of exploitation, because kin selection should favor individuals that imposed fewer costs on their kin. However, taking into account the gains of the exploited individual, allowing kin to exploit one's efforts may be less costly than allowing exploitation from non-kin. In this case, there may be higher frequencies of exploitative behaviours among related than unrelated individuals. In order to understand the net effect of genetic relatedness on intra-group exploitation, we developed a model that considers the inclusive fitness consequences of 'producing' (searching for food) and 'scrounging' (exploiting the food discoveries of others) when foraging with relatives, while simultaneously allowing individuals to show differential tolerance towards scrounging by kin versus non-kin. The model predicts that increased relatedness can lead to higher levels of exploitation when producers are kin-selected to allow scrounging from relatives but impose costs on unrelated scroungers, for example by being aggressive towards them. We tested this prediction empirically in captive zebra finches (*Taeniopygia guttata*) foraging either in flocks with full-siblings or in flocks of unrelated individuals. Flocks of related zebra finches had higher frequencies of scrounging and lower levels of aggressive interactions compared with flocks of unrelated zebra finches. The results suggest that producers may be kin-selected to allow relatives to scrounge. Surprisingly, although increased levels of scrounging are typically associated with a decrease in food patch discovery rate, groups of related individuals did not suffer any reduction in patch discovery rates compared with non-kin groups. This presumably arose because less time was spent in aggressive interactions in kin groups. Given that kin groups have patch discovery rates equal to those of non-kin groups while at the same time experiencing lower levels of aggressive interactions, there is a net benefit to grouping with kin, even when kin groups exhibit a higher frequency of exploitative behaviours.

5.2 Introduction

Group membership provides individuals with the opportunity to exploit resources produced or discovered by others. The exploitation of others' behaviour or efforts is known as "free-loading" in the field of economics, "tolerated theft" or "food-sharing in anthropology and "joining", "kleptoparasitism" or "scrounging" in behavioural ecology (see Giraldeau and Dubois 2008 and references therein). Examples of exploitative behaviours are both common and taxonomically widespread (Barnard 1984). Although exploitative behaviour may impose important costs on group members, in many cases, exploitation may be an inescapable consequence of group living (Giraldeau and Caraco 2000). Grouping with kin is believed to provide a means of mitigating some of the costs of exploitation by group members (Eckman et al. 2004; Frank 2003; Hamilton 1964). From the point of view of the exploiting individual, the net benefit of the exploitative behaviour is reduced when exploiting kin, due to a loss in inclusive fitness. Consequently, kin selection should favour a reduction in the frequency of exploitation.

However, from the point of view of the individual being exploited, the cost of exploitation is less when being exploited by kin, because the loss in direct fitness is at least partially offset by a gain in inclusive fitness. This may cause individuals to be more tolerant of exploitation by kin. If individuals impose sufficient costs on unrelated individuals that attempt to exploit them, it may lead to higher levels of exploitation in kin groups since the payoff for exploiting kin would tend to be greater than the payoff for exploiting non-kin. For example, in intra-specific brood parasites, if hosts are more likely to accept eggs from closely related individuals, the frequency of exploitation may be higher among kin because parasitizing kin yields a higher payoff than parasitizing non-kin (see Andersson 2001; Andersson and Åhlund 2000; López-Sepulcre and Kokko 2002). If kin selection leads to higher levels of exploitation, it is unclear whether there would be an overall advantage to grouping preferentially with kin. Given that the balance of costs and benefits to grouping are critical to understanding the evolution of sociality, it is also important to explore the consequences that genetic relatedness will have on the intensity of within group exploitation.

One form of exploitation which has been studied extensively in behavioural ecology is the usurpation of other individual's food discoveries (Giraldeau and Caraco 2000; Vickery et al. 1991). The economic consequences of such exploitative behaviour can be modeled as a producer-scrounger game, where "producer" refers to the tactic of actively searching for food, and "scrounger" refers to the tactic of searching for opportunities to exploit the food discoveries of others (Caraco and Giraldeau 1991; Giraldeau and Caraco 2000; Vickery et al. 1991). Although individuals can alternate between using both tactics, the tactics are mutually exclusive and cannot be performed simultaneously (Giraldeau and Caraco 2000).

Producer-scrounger models assume that the payoff to producer is larger than that to scrounger when producer is rare, and vice versa (Giraldeau and Caraco 2000). Consequently, at some intermediate frequency of producer and scrounger use, both tactics receive equal payoffs: a point known as the stable equilibrium frequency (SEF) (Morand-Ferron et al. 2007; Mottley and Giraldeau 2000). Groups converge on the SEF via behavioural adjustment of their investment in the alternative tactics (Barnard and Sibly 1981; Mottley and Giraldeau 2000). Increasing group size and increasing patch size both decrease the SEF of producer (Coolen 2002; Vickery et al. 1991), and scroungers impose a cost on all group members via a decrease in average foraging intake rate (Coolen 2002).

To date, no quantitative model has been developed to address the effect of genetic relatedness on the use of producer-scrounger foraging alternatives. As such, the influence of relatedness on producer-scrounger foraging remains unclear, with different studies making different *a priori* predictions for the effect of relatedness on producer-scrounger foraging decisions. One study predicts decreased scrounging among relatives (Vickery et al. 1991), while another predicts increased scrounging among relatives (McCormack et al. 2007), and two others argue that relatedness may either increase or decrease the frequency of scrounging (Ha et al. 2003; Tóth et al. 2009), depending on whether or not producers exclude unrelated scroungers from food patches. Here, we use Giraldeau and Caraco's (2000) modified two tactic version of Vickery et al.'s (1991) rate maximizing producer-scrounger foraging model and explore the inclusive fitness effects of foraging with kin on the SEF of scrounger. We believe that these apparent contradictions depend in part on whether models focus of the

producer or the scrounger's interests. It is important that social foraging predictions concerning inclusive fitness take into account concurrently the interests of both the producers and the scroungers. Because of this we model two scenarios: 1) scrounging is solely controlled by the scroungers' interests and so relatedness influences only the propensity of individuals to invest in exploitative behaviours, and 2) scrounging is the result of an interaction between producer and scrounger interests such that relatedness influences both the scroungers' propensity to exploit and the producers' propensity to tolerate exploitation. We then test which of these models best predicts the effect of relatedness on social foraging behaviour using a controlled aviary experiment with foraging zebra finches (*Taeniopygia guttata*).

5.3 The model

Vickery et al.'s (1991) rate maximizing model uses an individual's food intake as a surrogate for fitness. The model applies to a group of G foragers, where some proportion of individuals, p, play producer and the remaining individuals (1-p) play scrounger. Producers discover food patches containing F food items at rate of λ. Producers consume a items (the finder's advantage) before any scroungers arrive at the patch, where $0 \leq a < F$. The finder's advantage is fixed, and is an attribute of order of arrival at the patch, not of the individual. Thus, the finder's share can be defined as a/F. The remaining food, F-a, is shared equally between the producer and all the scroungers at the patch. The model assumes that all scroungers detect and exploit each scrounging opportunity and they all arrive at the patch synchronously.

Thus, the intake of a producer (I_p) over T time units of foraging is

(1a) $$I_p = \lambda T\left(a + \frac{F-a}{1+(1-p)G}\right),$$

and the intake of a scrounger (I_s) over the same time period is

(1b) $$I_s = \lambda TpG\left(\frac{F-a}{1+(1-p)G}\right).$$

The equilibrium proportion of producers in a group, $\hat{p}$, is found by setting the intake of producer equal to that of scrounger. Solving for $\hat{p}$ gives:

(1c) $$\hat{p} = \frac{a}{F} + \frac{1}{G}.$$

5.3.1 An inclusive fitness model of producing and scrounging under scrounger control alone

Here we hypothesize that inclusive intake rate of a forager is a currency of inclusive fitness. Inclusive intake requires that we take into account for each tactic its direct gains plus the effect of the tactic on the gains of others. For producer, inclusive intake will take into account the direct benefit from eating food it discovered plus indirect benefits from the feeding opportunity it provides to scroungers with whom the producer is genetically related by coefficient *r*. A producer's direct benefit over *T* time units of foraging is given by equation 1a, and its indirect benefit is equal to the intake it provides to scroungers, discounted by *r*. Therefore, the inclusive intake of a producer is:

(2a) $$I_{p(r>0)} = \lambda T\left(a + \frac{F-a}{1+(1-p)G}\right) + r\lambda T(1-p)G\left(\frac{F-a}{1+(1-p)G}\right).$$

A scrounger's direct gain from scrounging over *T* time units of foraging is given by equation 1b. A scrounger's indirect benefit is negative, as it consumes food that would otherwise have been eaten by others in the group. Thus, scroungers lose inclusive fitness as a result of their scrounging behaviour and the indirect component is the total intake of a scrounger over T time units (Eq. 1b) devalued by *r*. The inclusive intake of scroungers is:

(2b) $$I_{s(r>0)} = \lambda TpG\left(\frac{F-a}{1+(1-p)G}\right) - r\lambda TpG\left(\frac{F-a}{1+(1-p)G}\right)$$

The stable proportion of producer tactic use among groups of related foragers is determined by setting equation 2a equal to equation 2b. Solving for *p* gives:

(2c) $$\hat{p}_{(r>0)} = \frac{a}{F} + \frac{1}{G} + r(1 - \frac{a}{F}).$$

When inclusive intake is considered, the net effect on both tactics predicts that the equilibrium frequency of producer increases with genetic relatedness among players by a factor of $r(1\text{-}a/F)$ (Figure 5.1). The effect of relatedness will be strongest for small finder's shares (when producers get to monopolize only a small fraction of a food patch). Moreover, pure producer can exist as the only stable tactic over a broader range of finder's shares and group sizes than when group members are unrelated.

5.3.2 An inclusive fitness model of producing and scrounging based on producer control

Up to now we assumed that a producer was a tolerant victim of scroungers. Now we explore a situation where producer can be intolerant and impose a cost to scroungers. When a scrounger is related to the producer, its feeding imposes both a direct cost on the producer in terms of lost food and an indirect gain given the food is eaten by a relative. Consequently, producers may be more tolerant of scroungers to whom they are related than to non-related individuals. Here, we assume that producers only impose costs on unrelated scroungers and evaluate the consequences of this discrimination on the SEF of producer.

When foragers are unrelated, we assume that producers are able to impose costs on scroungers, for example via aggression. We assume that the cost paid by the producer is less that the cost imposed upon a scrounger, and the equation takes into account the net cost imposed on scroungers. In such a situation the producer's intake remains as in equation 1a but the scrounger's intake is reduced by some proportion (c) of the total value of the scrounged patches (eq. 1b). The intake of a scrounger becomes:

(3a) $$I_{s(costs)} = \lambda TpG(1-c)\left(\frac{F-a}{1+(1-p)G}\right)$$

The stable equilibrium frequency of producer in groups of unrelated individuals when producers impose costs on scroungers can be found by setting equation (1a) equal to equation (3a). Solving for p gives:

(3b) $$\hat{p}_{(costs)} = \frac{a/F + 1/G}{1 - c(1 - a/F)} \ .$$

When producers are able to impose costs on scroungers, the model predicts that the equilibrium frequency of producer increases (Figure 5.2). The increase in the frequency of producer is greatest when costs imposed on scroungers (c) are high. Furthermore, the magnitude of the effect of such costs is greatest for small finder's shares (when producers get to monopolize only a small fraction of a food patch).

Imposing costs on unrelated scroungers increases the equilibrium frequency of producer in non-kin groups. If at the same time, kin groups experience an increase in the equilibrium frequency of producer due to the indirect fitness cost of scrounging from kin, then under some conditions, imposing costs on unrelated scroungers can lead to a higher frequency of exploitation in kin groups. If producers impose costs on unrelated scroungers, but do not impose costs on related scrounger, then the frequency of exploitative behaviours in kin groups will be greater than that in non-kin groups whenever equation 2c < equation 3b. Over a wide range of parameter values (a/F, G and r), small costs (c) are sufficient to generate higher levels scrounging in kin groups compared with non-kin groups.

5.4 Testing the models experimentally

Here we test the prediction that kin groups can show higher frequencies of the exploitative foraging tactic when producers impose costs on unrelated scroungers. To do this, we formed flocks of full-siblings and flocks of unrelated zebra finches and we recorded both the frequency of scrounging and the frequency of aggressive interactions. Zebra finches engage in social foraging in the wild (Zann 1996), and have been used as a extensively in laboratory studies of producer-scrounger foraging (Giraldeau and Dubois 2008 and

references therein). They are also easy breed in captivity (Zann 1996), making it possible to create flocks of individuals of known relatedness. Zebra finches also fight in defence of food (Immelmann 1982), and are able to discriminate between kin and non-kin (Burley et al. 1990), which suggests they may be able to show differential tolerance towards kin versus non-kin scroungers.

5.5 Methods

5.5.1 Study subjects and aviaries

Breeding took place between January and June 2008. Adult zebra finches were paired randomly and each pair was housed in an individual cage (57 × 29 × 42 cm) to allow for unambiguous parentage assignment. Each cage contained two perches, one reed nest and nesting materials. Birds were maintained on a 12h:12h light:dark cyle (lights on from 6h00 to 18h00) at temperatures between 22 and 24°C. During breeding and outside of experimental periods, birds had ad libitum access to water, vitamin-supplemented commercial millet seed mixture, cuttlefish bone, and crushed oyster shells. Additionally, birds were provided with fresh fruits and vegetables three times per week, and a protein supplement once per week.

A total of 10 couples produced 53 offspring. Chicks were removed from their natal cage at independence (42.3 ± 0.7 days after hatching), and housed in single sex groups. From these offspring, we formed 10 mixed-sex flocks of 5 birds each. 'Related' flocks (N = 5) were comprised of full siblings from 2 to 3 separate clutches, and 'unrelated' flocks (N = 5) were comprised of individuals from 5 different families. Within each flock, individuals were provided with a unique leg flag colour. Birds were not used in experiments until they reached at least 90 days of age to ensure that they were developmentally mature (Zann 1996).

5.5.2 Experimental procedure

During experiments, flocks were placed into indoor aviaries (1.5 × 3.8 × 2.3 m high). Each aviary contained two large perches and a foraging grid that consisted of 2 side by side

plywood boards with a combined dimension of 2.2 by 1.1 m, in which a total of 200 wells 1.5 cm in diameter, 0.8 cm deep, and spaced at 10 cm intervals were drilled. Foraging grids were placed on tables approximately 90 cm above the aviary floor, which allowed a seated observer to videotape the birds through a one-way mirror using a digital video camera mounted on a tripod. The foraging grid was covered by a sheet of black plastic at all times except during the foraging trials. The perches were placed at the far end of the aviary so that birds could not see directly into the wells from the perches, but had to fly down to the foraging grid to search for food.

Birds were given 2 d to become familiar with the aviaries. Food was removed at 18h00 on the evening of the second day and each evening thereafter (evenings 2 through 9). Trials commenced at 8h00 the following mornings (days 3 through 10). Thus, birds were deprived of food during the 12h dark phase, plus an additional 2h after lights on, durations that were necessary given that zebra finches store seeds in their extensible crops for overnight use.

Foraging trials were conducted for 8 d (days 3 through 10) 5 times per d at 1 h intervals. During each foraging trial, 10 millet seeds were placed in each of 20 randomly selected wells. This seed distribution results in a finder's share (a/F) of roughly 0.2 (personal observation). Trials typically lasted circa 5 min, after which time, all the patches on the foraging grid had been exploited and the birds returned to the perches. Birds were given ad libitum access to food following the final foraging trial each day (from 12h40 to 18h00).

Each foraging trial was videotaped as the observer (KJM) called out the location of individuals into the audio channel of the videotape recorder to facilitate the identification of the individuals during the playbacks from which data were recorded.

5.5.3 Video analysis

Each video file of foraging trials was assigned a coded name from 001 to 400 in order to allow a single observer (KJM) to score the videos blind to relatedness treatment.

Videos were scored in random order using Noldus Observer 5.0 Video Pro. The finding and joining events of each flock member were scored for the first 3 min of each trial. A finding event was defined as an event where the focal individual was the first to encounter and feed at a patch, and is the outcome of investing in the producer tactic. A joining event was defined as an event where the focal individual moved towards a patch with at least one other bird already there, irrespective of whether it subsequently fed from the patch or not. Joining is the outcome of investing in the scrounger tactic. We also scored the occurrence of aggressive interactions. Aggressive interactions included chases, beak fences, and postural displays (Adkins-Regan and Robinson 1993). Aggressive interactions were scored for the entire duration of each filmed trial (mean 5.5 min, range: 5-20 min) because these events were less frequent than finding and joining events.

5.5.4 Statistical analyses

All statistical analyses were carried out using R v.2.8.0 (R Development Core Team 2008). We used a generalized linear mixed model with a binomial error distribution to evaluate the proportion of joining events as a function of 'Treatment' ('Related' or 'Unrelated'), 'Trial number' (1 through 40), and their interaction. The model we developed, and other models of producer-scrounger foraging, predict the SEF of tactic use within foraging groups, without explicitly treating the time required for groups to converge on the equilibrium. We included 'Trial number' in the model in order to account for the fact that the frequency of tactic use may have been changing over the course of repeated trials while flocks converged on the SEF. The response variable was defined as a two-column matrix composed of the number of patches joined and the number of patches found within a trial for the whole flock (using the 'cbind' function). This function takes into account both the proportion of joining events, and the total number of events used to estimate that proportion.

Data on the frequency of aggression (number of aggressive interactions per minute) were analyzed using a generalized linear model with a quasi-Poisson error distribution. We included 'Treatment' ('Related' or 'Not-related'), 'Trial number' (1 through 40) and the proportion of joining (total joining events/total finding events) as fixed effects, as well as

their interaction. 'Trial number' was included in the model to account for possible changes in aggression levels resulting from increased familiarity between flock mates over time. Proportion joining was included because higher frequency of joining may result in more opportunities for aggression because flock mates would tend to be closer to each other when multiple individuals feed from the same patch.

We also tested whether groups of kin and non-kin differed with respect to their patch discovery rates using a generalized linear mixed model ('glm' function from the 'lme4' library), with a quasi-Poisson error distribution. We included 'Treatment' ('Related' or 'Unrelated'), 'Trial number' (1 through 40) and their interaction as fixed effects. 'Trial number' was included in the model to account for possible changes in foraging efficiency associated with increased experience with foraging on the grids or changes in frequency of producer-scrounger alternatives. The time required for flocks to locate the first 10 patches was used as the response variable to reduce any effects of patch depletion.

All models included 'Flock' as a random effect (~1|Flock) to account for non-independence of errors associated with the repeated observations of the same flocks. Models were simplified by removing non-significant interactions ($p > 0.05$) in a reverse-stepwise manner, and significant interactions were interpreted based on the effect sizes estimated by the minimally adequate model. Values presented throughout the text are means ± 1 standard error.

5.6 Results

We tested whether relatedness influenced the use of the scrounger tactic, and found a significant interaction between 'Treatment' and 'Trial number' ($z = 1.96$, $p = 0.05$) on the frequency of joining. During the first several trials, flocks of related and unrelated individuals showed similar joining frequencies (Figure 5.3). Estimated effects sizes indicate that while all flocks decreased their frequency of joining over successive trials, this decrease was less pronounced in flocks of related individuals (Table 5.1). Thus, after 40 trials, flocks of related

individuals had joining frequencies more than 20% higher than flocks of unrelated individuals (0.39 versus 0.31).

We observed a total of 2059 aggressive interaction during 2273 min of observation. There was a significant effect of 'Treatment' on the frequency of aggressive interactions ($t_{1,396} = -6.29$, $p < 0.0001$); flocks of unrelated individuals had approximately two times higher frequencies of aggression compared with flocks of related individuals (Figure 5.4). There was also a small but significant effect of 'Trial number' ($t_{1,396} = -2.13$, $p = 0.034$) on the frequency of aggression, with the frequency of aggression decreasing slightly across trials. Finally, there was a significant effect of the proportion joining ($t_{1,396} = -4.16$, $p < 0.0001$) on the frequency of aggression. Controlling for 'Treatment' and 'Trial number', lower frequencies of aggression were associated with higher joining frequencies (Table 5.2). All interactions were non-significant (all $p > 0.10$).

Finally, we tested whether groups of kin and non-kin differed with respect to their patch discovery rates, the interaction between 'Trial number' and 'Treatment' for the time required to locate 10 patches was not significant ($p > 0.10$), and was removed from the model. However, there was a significant effect of trial number on the time required to locate 10 patches ($t_{1,397} = -11.19$, $p < 0.0001$), which decreased with increasing trial number. There was no effect of 'Treatment' ($t_{1,397} = -0.16$, $p = 0.87$) on the time required to find 10 patches (Table 5.2, Figure 5.5).

5.7 Discussion

Under scrounger-control, kin selection generally favours a reduction in the frequency of exploitation within a group (Hamilton 1964), however, producers also affect whether animals can scrounge or not, and they may be kin-selected to tolerate exploitation of their efforts by relatives, but not non-relatives. Producer-control scenarios predict a higher frequency of exploitation in kin groups compared with non-kin groups (Frank 1995; Frank 2003; Wenseleers et al. 2004; Wenseleers and Ratnieks 2006). The model we developed here shows that producers that can impose even small costs on scroungers can, by their

discrimination between related and unrelated scroungers, favour higher levels of exploitation in kin groups compared to non-kin groups. Social foraging in flocks of zebra finches conformed to a producer-controlled system because kin groups were characterized by a higher frequency of scrounger. In line with this interpretation, zebra finches were less tolerant of scrounging by non-kin resulting in a nearly 2-fold higher rate of aggression within non-kin compared to kin groups.

Scrounger levels were initially similar for both related and unrelated flocks, and all flocks decreased their use of scrounger across trials. This is similar to results from another study on zebra finches where individuals with prior experience with the foraging conditions had a higher use of producer than those with no prior experience (Beauchamp 2000a). The decline in scrounging may be due to increased experience resulting in an increase in foraging efficiency, which itself favors a higher use of the producer tactic (Beauchamp 2006). However, in our experiments, the decrease in scrounger was greater among non-kin groups such that by the end of 40 trials, groups of related individuals had a significantly higher use of the scrounger tactic compared with groups of unrelated individuals.

We interpret the observation of higher levels of scrounging in kin groups as evidence that producers exert control over scrounging decisions. Consistent with this, we observed nearly 2-fold higher rates of aggression in non-kin groups compared with kin groups, which suggests that, in this system, producers have been kin-selected to be more tolerant of scrounging by kin. Increased rates of aggression may be used to reduce the benefit of scrounging, and consequently, to reduce the frequency of scrounging. This would occur if individuals distanced themselves from flock mates to decrease their probability of being the victim of an aggressive interaction. Because increased distance between individuals decreases the benefit of joining (Beauchamp 2008), this in turn may result in a reduced frequency of joining. Consistent with this, within treatment groups (kin versus non-kin) higher levels of aggression were associated with reduced joining frequencies.

A general result from both theoretical and empirical studies of the frequency-dependence in producer-scrounger games is that as the frequency of the scrounger tactic

increases, the group level patch discovery rate decreases, because fewer individuals are engaged in actively searching for food (Coolen 2002; Giraldeau and Caraco 2000). Thus, based on the finding that flocks of related individuals have a higher frequency of joining, we might expect that they will also be less efficient at finding patches. However, this was not the case, as there were no differences in the time required to locate 10 food patches for flocks of kin versus non-kin. A possible explanation for this finding is that searching is less efficient in groups of unrelated foragers because a larger proportion of time in spent engaged in aggressive interactions (Sirot 2000). Thus, despite experiencing a higher frequency of exploitative behaviours, kin groups may still enjoy a net benefit over non-kin groups because they achieve the same foraging intake rate but pay lower costs associated with aggressive interactions.

5.7.1 The occurrence of producer-control versus scrounger control

At least four earlier studies have tested for an effect of relatedness on producer-scrounger foraging, with mixed results (Ha et al. 2003; King et al. 2009; McCormack et al. 2007; Tóth et al. 2009). None of the studies found a clear effect of relatedness on the frequency of the exploitative foraging tactic, scrounger. Several factors may account for the differences in results, including differences in the relatedness threshold used, group size, finders' share, and whether joining is under scrounger- or producer-control, all of which are predicted to influence the SEF of scrounger (this study). However, two studies reported higher frequencies of aggression among unrelated individuals, which suggests that joining may be under producer-control in these systems as well. In both northwestern crows (*Corvus caurinus*) (Ha et al. 2003) and house sparrows (*Passer domesticus*) (Tóth et al. 2009), scrounging attempts between non-kin were more likely to involve aggression than scrounging attempts between kin.

Producer-scrounger relationships are not restricted to group foraging situations (Barnard 1984) and several earlier studies have investigated the role of relatedness on the frequency of producer and scrounger tactics for other forms of exploitative behaviour. The model predictions appear quite general to other producer-scrounger relationships despite

differences in how costs and benefits are apportioned between producers and scroungers for various types of exploitative behaviours. In scrounger-controlled systems, the general finding for organisms ranging from bacteria to higher vertebrates is that increasing relatedness among group members decreases the frequency of exploitation (Buss 1982; Castillo et al. 2005; Diggle et al. 2007; Fiegna and Velicer 2005; Griffin et al. 2004; Hudson et al. 2002; Schneider 1996; Schneider and Bilde 2008; Semel and Sherman 2001; Zink 2000). However, in producer-controlled systems higher levels of exploitative behaviours can be favoured in kin groups (Andersson 2001; López-Sepulcre and Kokko 2002).

The importance of considering the extent to which an individual's behavioural decisions are the product of their own interests, or enforced by the interests of others' may have widespread application for understanding animal behaviour. For example, when group membership is determined under free-entry, increasing relatedness favours smaller group sizes, but when group members restrict entry to the group, increasing relatedness favours larger group sizes (Giraldeau and Caraco 1993; Higashi and Yamamura 1993). Similarly, the optimal level of reproductive skew in groups is a function not only of the mean relatedness among group members, but is also dependent on whether dominants, subordinates, or both, control reproduction (Langer et al. 2004; Reeve et al. 1998).

5.7.2 Implications for group formation

Neither the models nor the experiments presented here specifically address the underlying process of group formation (Giraldeau and Caraco 2000). However, the empirical results suggest that groups of relatives may have higher net benefits for a given group size and finder's share than groups of non-relatives, even when groups of kin have a higher frequency of exploitative behaviours. Measures of individual fitness in kin groups versus non-kin groups would be needed to address this directly.

However, it is also important to note that the model and empirical results reported here are based on a simplified scenario where groups are comprised either of all kin or non-kin. Although this simplification was useful for demonstrating differences in the tendency for

individuals to exert control against kin versus non-kin scroungers, a more realistic scenario in wild populations would be for groups to be comprised of a mixture of individuals of varying degrees of relatedness (Avilés et al. 2004 and references therein). In this situation, if producers are most tolerant of their closest kin joining them at food discoveries, this may result in scrounger preferentially joining kin, resulting in assortative sub-groups forming within the larger foraging group. Although there is some evidence of differential tolerance of kin versus non-kin in heterogeneous groups (Ha et al. 2003; Tóth et al. 2009), more detailed studies are warranted which control for group size and finder's share, both of which are known to influence producing and scrounging decisions.

5.7.3 Conclusion

This study emphasizes the importance of identifying who controls the frequency of exploitation in order to be able to predict the effect of relatedness on the frequency of exploitation, and consideration of whether an individual's behavioural decisions are the product of their own interests, or enforced by the interests of others' may have widespread application for understanding animal behaviour. Factors including the distribution of food, the cost of fighting, competitive asymmetries between finder's and joiners, and the finder's advantage all influence the net benefit to producer for exerting control over joining (Dubois and Giraldeau 2007; Dubois et al. 2003; Sirot 2000). Depending on the values of each of these parameters, either producer-controlled or scrounger-controlled joining can be predicted (Dubois and Giraldeau 2007). Studies of social foraging should begin to explicitly address who controls joining because it can critically influence the predicted outcome for the level of exploitation in groups.

5.8 Acknowledgments

These experiments conform to guidelines of the Canadian Council for Animal Care and were approved by the University Animal Care Committee (0108-601-0109).We are grateful to Neeltje Boogert for her help with the breeding of the zebra finches, Jan Wijmenga for constructing the foraging grids, Neeltje Boogert, Julie Morand-Ferron and Bill Vickery for

comments on earlier versions of the manuscript, and members of the Giraldeau lab for helpful discussions. KJM was supported by an NSERC graduate scholarship and an NSERC Discovery grant to L.-A.G.

Table 5.1: Estimated effect sizes ± standard error, z-values and p-values for fixed effects in GLMMs with a binomial response (number of patches scrounged, number of patches produced).

Source of variation	**Estimate ± se**	*z*	*p*
Dependent variable: (joining events, finding events)			
Treatment[±]	0.085 ± 0.229	0.37	0.71
Trial number	-0.026 ± 0.002	-9.95	<0.001
Treatment[±] × *Trial number*	0.0070 ± 0.0036	1.96	0.050

[±]Reference value for treatment is 'Unrelated'

Table 5.2: Estimated effect sizes ± standard error, t-values and p-values for fixed effects in GLMM with quasi-Poisson error distributions. Non-significant ($p > 0.05$) interactions were removed in a reverse-stepwise manner, and minimally adequate models are presented.

Source of variation	**Estimate ± se**	*t*	*p*
Dependent variable: Aggressive interactions / min			
Treatment[±]	-0.74 ± 0.12	-6.29	< 0.001
Trial number	-0.011 ± 0.005	-2.13	0.034
Proportion of joining	-1.95 ± 0.47	-4.16	<0.001
Dependent variable: Time (sec) to find 10 patches			
Treatment[±]	-0.008 ± 0.049	-0.16	0.88
Trial number	-0.024 ± 0.002	-11.19	<0.0001

[±]Reference value for treatment is 'Unrelated'

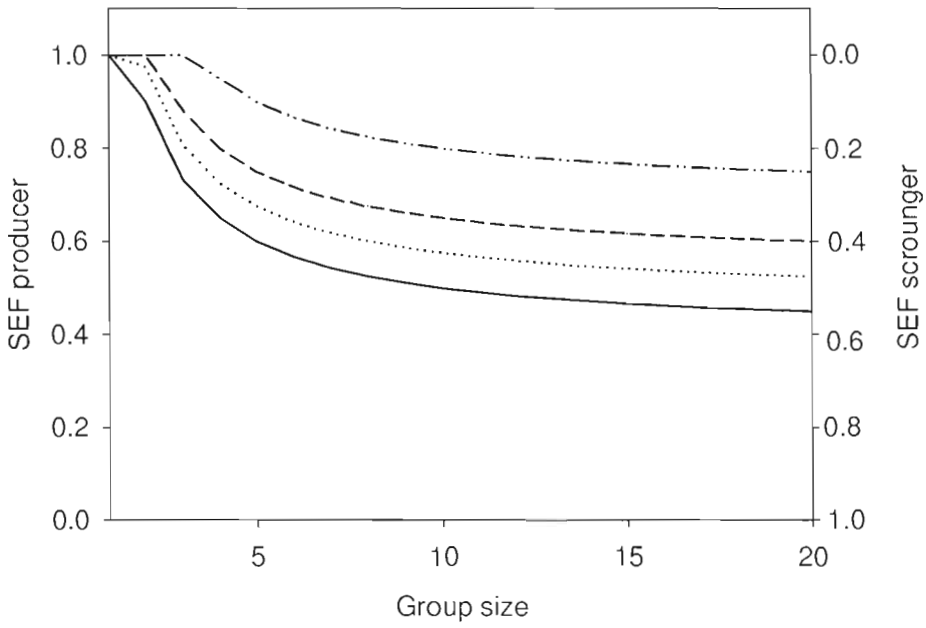

Figure 5.1: Predicted stable equilibrium frequency (SEF) of tactic use as a function of the mean relatedness coefficient among group members (r) and group size (G). Proportion producer (p) is shown on the left y-axes, proportion scrounger ($1-p$) is shown on the right y-axes. $r = 0$ is plotted with a solid line, $r = 0.125$ with dotted lines, $r = 0.25$ with dashed lines, and $r = 0.5$ with alternating dashed and dotted lines. In this figure, $a/F = 0.4$.

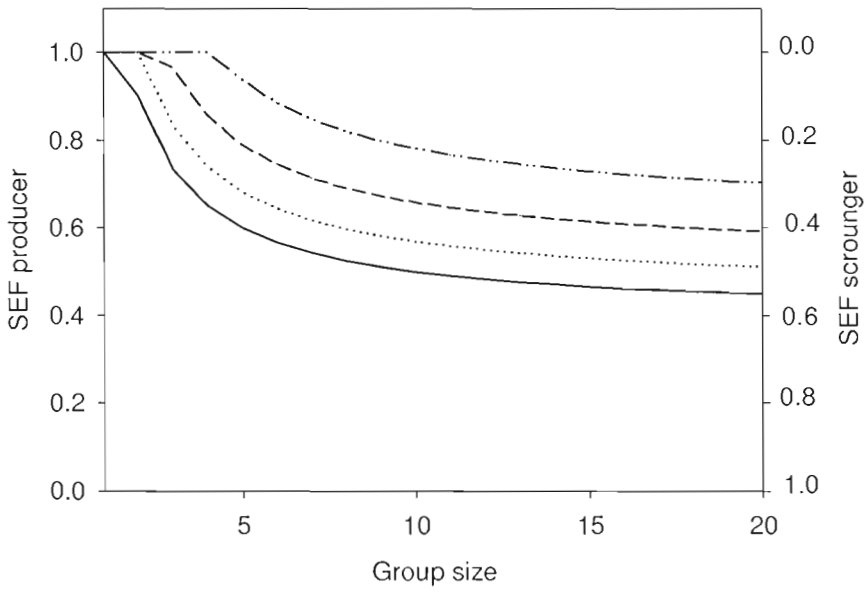

Figure 5.2: Predicted stable equilibrium frequency (SEF) of tactic use as a function of costs imposed on unrelated scroungers (c) and group size (G). Proportion producer (p) is shown on the left y-axes, proportion scrounger (1-p) is shown on the right y-axes. Costs (c) are expressed relative to the value of the scrounged patched. $c = 0$ is plotted with a solid line, $c = 0.2$ with dotted lines, $c = 0.4$ with dashed lines, and $c = 0.6$ with alternating dashed and dotted lines. In this figure, $a/F = 0.4$

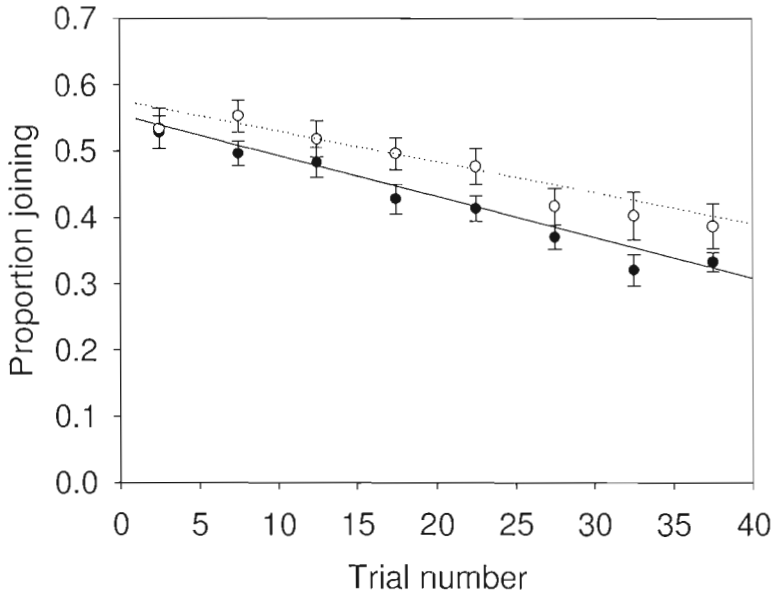

Figure 5.3: Proportion of joining events as a function of relatedness and trial number. Flocks of unrelated zebra finches are represented by solid circles and a solid line; flocks of related zebra finches are represented by empty circles and a dotted line. The best fit lines were calculated from the GLMM, and the data presented are means ± se calculated over 5 trials (ie trial 1-5, trials 6-10, etc.).

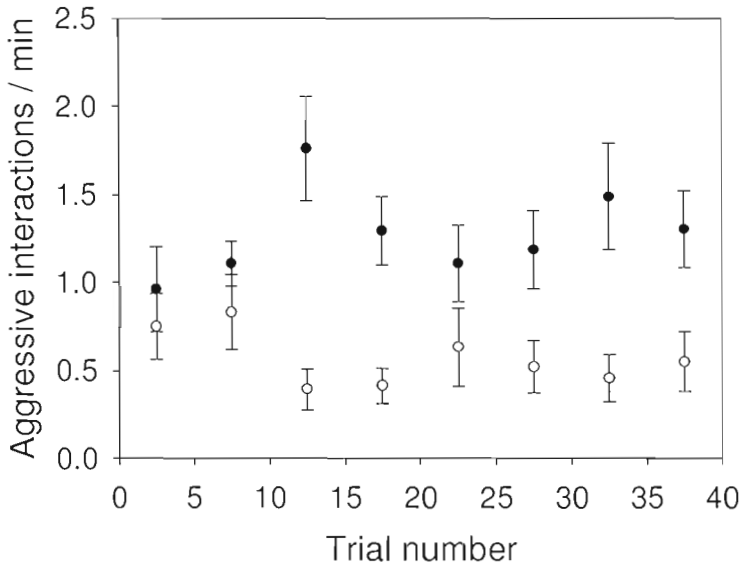

Figure 5.4: Frequency of aggressive interactions as a function of relatedness and trial number. Flocks of unrelated zebra finches are represented by solid circles and a solid line; flocks of related zebra finches are represented by the empty circles and a dotted line. The best fit lines were calculated from the GLMM, and the data presented are means ± se calculated over 5 trials.

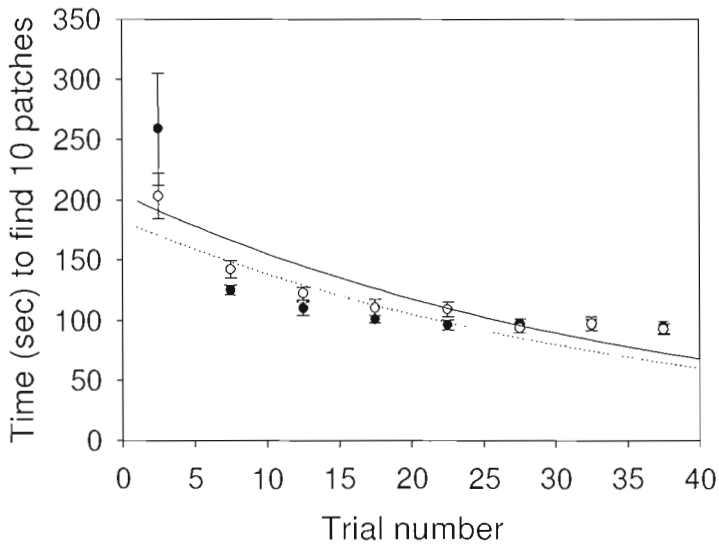

Figure 5.5: Search efficiency of flocks (measured as time required to find 10 patches) as a function of relatedness and trial number. Flocks of unrelated zebra finches are represented by solid circles and a solid line; flocks of related zebra finches are represented by empty circles and a dotted line. The best fit lines were calculated from the GLMM, and the data presented are means ± se calculated over 5 trials.

CHAPTER 6
GENERAL CONCLUSION

6.1 Synthesis

Social foraging is one of the best-studied systems where individuals are able to use alternative behavioural tactics (Giraldeau and Caraco 2000). Although there have been several indications that individual differences in tactic use may be important (Barta and Giraldeau 1998; Beauchamp 2001), few studies have systematically explored factors that may underlie individual variation in tactic use (but see Beauchamp 2000b; Beauchamp 2006; Thibaudeau 2004), despite the fact that phenotype limited tactic use may have important implications regarding inter-individual variation in fitness (Parker 1982). In this thesis, I identified three phenotypic traits that influence social foraging tactic use in the zebra finch (*Taeniopygia guttata*): vulnerability to predation, basal metabolic rate (BMR), and body condition (an index of fat reserves).

I tested whether individual vulnerability to predation influenced social foraging tactic use (Chapter 2). Based on differences in head posture and spatial location within the group associated with producer and scrounger tactics, I predicted that higher vulnerability to predation should favour an increased use of the scrounger tactic. In ground feeding birds, individuals hop with the head oriented downward when producing, and hop with the head oriented upward when scrounging (Coolen et al. 2001). Thus, searching for feeding opportunities as a scrounger may provide greater inherent vigilance (Barbosa 1995; Elgar et al. 1986; FitzGibbon 1989; Lima and Bednekoff 1999), and therefore be more valuable to individuals with a higher individual vulnerability. Furthermore, 'scroungers' are more likely to be found in central positions in the group (Barta et al. 1997; Flynn and Giraldeau 2001), which tend to be safer compared with edge positions (Elgar 1989; Keys and Dugatkin 1990). I used wing-loading manipulations to experimentally increase an individual's vulnerability to

predation, because increased wing loading reduces escape flight performance (Burns and Ydenberg 2002; Kullberg et al. 2005; Marchetti et al. 1995; Senar et al. 2002). As predicted, the increase in wing-loading resulted in an increased use of the scrounger foraging tactic.

The effect of vulnerability to predation on the use of the scrounger tactic was predicted *a priori* based on two possible non-exclusive mechanisms: 1) that the head up foraging posture associated with scrounging was compatible with anti-predator vigilance, and 2) the greater tendency for scrounger to occupy central positions in groups provided greater safety. Determining which of these mechanisms underlies the observed relationship between vulnerability to predation and tactic use will require experiments that break the association between these two factors. This could be done for example by providing linear foraging grids, which reduce the opportunity to be 'centrally' located within groups. Hence, the scrounger tactic would be associated with more head up foraging postures, but not with central locations in groups. Alternatively, food patches could be provided on small platforms such that both producers and scroungers search with their heads up.

I also tested whether individual differences in BMR influence tactic use decisions (Chapter 3). At the stable equilibrium frequency (SEF), producer and scrounger tactics are assumed to receive equal rewards on average, but the variance for producer is greater than that for scrounger (Koops and Giraldeau 1996; Wu and Giraldeau 2004). Variance-sensitive foraging theory predicts that when individuals run the risk of experiencing an energetic shortfall, they should prefer the more predictable (less variable) option early in the day (Barta and Giraldeau 2000). Previous studies have tested variance-sensitive foraging decisions in a producer-scrounger context using experimental manipulations of energy state (Lendvai et al. 2004; Lendvai et al. 2006; Wu and Giraldeau 2004). However, individuals may also have consistent differences in their probability of energetic shortfall based on differences in their basic energy requirements, ie) basal metabolic rate (BMR). I assumed that all else being equal, high BMR individuals may be at a greater risk of energetic shortfall compared with low BMR individuals. Consequently, I predicted that high BMR individuals would have a higher use of the scrounger tactic early in the day compared with low BMR individuals. Consistent with this, high BMR individuals did have a higher use of the scrounger tactic

compared with low BMR individuals. This study was the first to show that variation in BMR within a species correlates with differences in foraging behaviour. However, I also manipulated energetic state by changing food availability, and this had no effect of the use of producer-scrounger alternatives. Thus, whether BMR related differences in tactic use are the result of variance-sensitive foraging decisions, or some other mechanism remains unclear. However, I also recorded significant BMR-related differences in mass trajectories: individuals with higher BMR's consistently gained mass in the low food treatment, while low BMR birds lost mass. This result is strong evidence of unequal payoffs to individuals in a producer-scrounger context.

In Chapters 2 and 3, I show that tactic use is related to at least two different state variables: vulnerability to predation and BMR. Because various aspects of individual state are heritable, including BMR (Rønning et al. 2007), observed tactic use may also be heritable (Gross and Repka 1998a; Gross and Repka 1998b). I looked for evidence of heritability in social foraging behaviour by testing for family-related differences in tactic use, where families were comprised of full-siblings. I also tested for family-related differences in a measure of individual state which is believed to influence the use of producer and scrounger alternatives: body condition. I found that body condition scores differed significantly between families. This is consistent with the notion that body-condition is heritable, as has been reported for numerous other species (Dechow et al. 2002; Gosler and Harper 2000; Merilä et al. 2001; Schulte-Hostedde et al. 2005). Earlier studies have shown that an experimental decrease in body condition leads to higher use of the scrounger tactic (Lendvai et al. 2004; Lendvai et al. 2006). In this study, I show that natural variation in body condition scores were correlated with tactic use: individuals with lower body condition scores had a higher use of the scrounger tactic. Finally, I recorded significant family-related differences in the use of producer and scrounger alternatives. These results are consistent with heritability in observed tactic use resulting from an inheritance of individual state, in this case body condition, which itself influences tactic use. However, the family-related differences in body-condition and tactic use may be due to genetic, early environment effects, and/or shared parental effects, all of which were shared between full-siblings in this experiment. Future experiments aimed at disentangling the genetic versus environmental and parental

components could be carried out, and would require a cross-fostering design for clutch rearing.

I also developed a model (Chapter 5) which addressed how relatedness among group members should influence tactic use. I considered two scenarios: 1) foragers only adjust their investment in producing and scrounging as a function of relatedness, and 2) foragers adjust their investment in producing and scrounging, and exhibit different degrees of tolerance towards scroungers as a function of relatedness. Consistent with kin selection theory, the model predicted that the frequency of the exploitative tactic (scrounger) will decrease with increasing relatedness among group members when foragers only adjust their investment in producer-scrounger tactics as function of relatedness. However, when foragers are able to adjust their investment in producer-scrounger alternatives while simultaneously exhibiting differences in their level of tolerance towards scroungers as a function of mean group relatedness, the prediction reversed. When producers impose even small costs on non-related scroungers, groups of kin are predicted to have a higher frequency of scrounger. I tested the model predictions by comparing the frequency of scrounging and the frequency of aggressive interactions between groups of full-siblings and groups of unrelated individuals. I found that kin groups had a higher frequency of scrounging, but a significantly lower frequency of aggressive interactions than did non-kin groups. These results suggest that zebra finches conform to a producer-controlled system and highlight the importance of identifying who controls the frequency of exploitation in groups. Future studies of social foraging should explicitly address who controls joining because it can critically influence the predicted outcome of social foraging interactions.

6.2 Implications and future directions

The results of this research have yielded several new insights into the factors underlying inter-individual variation in tactic use. Individuals will adjust their investment in producer scrounger alternatives in response to a change in their individual state (such as vulnerability to predation). Furthermore, natural variation in state variables, including metabolic rate and body condition, are related to individual differences in producer-scrounger

tactic use. The finding that tactic use decisions in a producer-scrounger game are dependent on individual state variables may have important implications for individual variation in fitness, behavioural flexibility, and group formation decisions.

6.2.1 Inter-individual variation in fitness

In one of the first formal tests of producer-scrounger foraging, Barnard and Sibly (1981) observed that the foraging intake rate of house sparrows (*Passer domesticus*) differed between individuals. Individuals with a higher propensity to scrounge had a higher foraging intake rate than 'producer' individuals under several different group compositions (Barnard and Sibly 1981). This is in sharp contrast with the prediction that all individuals should receive equal payoffs when tactic use is strictly frequency dependent (Giraldeau and Caraco 2000; Vickery et al. 1991). Although it is unclear why individuals differed in their tactic use under a given set of conditions (group size, group composition, etc.), phenotypic-constraints would provide an explanation for the observed differences because under phenotype-limited tactic use, payoffs are expected to be equal within, but not between, phenotypes (Repka and Gross 1995).

The results presented in Chapter 3 provide direct evidence that phenotype-limited tactic use is associated with inter-individual variation in foraging payoffs. Individuals with high BMRs had a higher use of the scrounger tactic compared with low BMR individuals. High BMR individuals also gained mass across the foraging trials when food abundance was high, while low BMR individuals were only able to maintain mass under the same conditions. This suggests that high BMR individuals are at an advantage over low BMR individuals in high food conditions.

In order to understand the overall effect of phenotype-limited tactic use on individual variation in fitness, measurements of foraging intake rate should be compared under a wider range of conditions. For example, in the low food treatment, there were no differences between high and low BMR individuals. This may indicate that low BMR individuals are less sensitive to changes in food abundance. To test this, flocks could be subjected to lower food

abundance conditions, and we would predict that low BMR individuals would outperform high BMR individuals (Figure 6.1a). If this is the case, then the fitness expectations of high and low BMR individuals may balance out across situations, such that no one phenotype has a consistent fitness advantage over the other. Alternatively, at very low food abundances, high and low BMR individuals may perform equally poorly (Figure 6.1b). In this scenario, high BMR individuals would be expected to have an overall fitness advantage, since they never receive lower fitness payoffs than low BMR individuals, but under some circumstances receive higher fitness payoffs. A better understanding of phenotypic constraints on tactic use decisions will be important for understanding how, why and when individual variation in fitness will exist.

6.2.2 Behavioural plasticity

Given that individual state influences tactic use, and that some measures of individual state can be consistent throughout the lifetime of an individual (Bech et al. 1999; Berteaux et al. 1996; Hõrak et al. 2002; Labocha et al. 2004; Rønning et al. 2005), or even be heritable (Blanckenhorn and Hosken 2003; Boag and Alway 1981; Gosler and Harper 2000; Merilä et al. 2001; Phillips and Furness 1998; Rønning et al. 2007), individual differences in behaviour may be consistent across a wide range of contexts. Indeed, several studies have found that individuals do show consistent differences in their use of producer-scrounger alternatives (Beauchamp 2001; Morand-Ferron et al. 2007; Thibaudeau 2004). One avenue for future research would be to explore the implications of consistent individual differences in behaviour for behavioural plasticity.

Consistency in individual behaviour is often associated with limited behavioural plasticity (Sih et al. 2004a; Sih et al. 2004b). In a producer-scrounger foraging context, limited behavioural plasticity could occur if individual state variables not only favour the use of one tactic, but restrict the use of the alternative tactic. For example, higher intrinsic vulnerability to predation favours a higher use of the scrounger tactic, likely because it provides anti-predator benefits such as incidental vigilance and/or safer spatial location in the group (Chapter 2). However, because of their need to obtain anti-predator benefits while

foraging, individuals with a high intrinsic vulnerability to predation may never play pure producer when foraging in a group. Similarly, in some species, subordinate individuals are more likely to use the producer tactic compared with dominants because their low competitive efficiency reduces the payoff they can receive from scrounging compared with a dominant individual (Barta and Giraldeau 1998; Lendvai et al. 2006; Liker and Barta 2002; Thibaudeau 2004). This may limit the ability of subordinates to ever play pure scrounger, even when environmental conditions call for a higher use of the scrounger tactic.

Another possibility is that individual behavioural plasticity may not only be limited, but may also differ between individuals. Although we can predict that more vulnerable individuals may be restricted in their ability to use the producer tactic, there is no *a priori* reason to predict that the least vulnerable individuals will be limited in their ability to play scrounger. Similarly, there is no reason to expect that dominant individuals will be limited in their ability to play producer. Such asymmetries in the extent to which different individuals are restricted in their use of alternative tactics may lead to individual differences in behavioural plasticity. If the degree of behavioural plasticity shown by an individual is influenced by the same factors that influence tactic use, this suggests that consistent individual differences in behaviour and individual differences in behavioural plasticity should be studied concurrently (Dingemanse et al. 2010).

It would be possible to study the behavioural flexibility of individuals, as well as differences in the behavioural flexibility of individuals, by comparing tactic use of focal individuals under conditions that favour higher or lower levels of scrounging and comparing the degree of behavioural adjustment of different individuals. This type of design has been used already to test individual flexibility of tactic use in house sparrows. Focal individuals did not adjust their own tactic use in response to the frequency of tactic use in the groups in which they were placed (Barnard and Sibly 1981). Given the frequency dependence between payoffs, the failure to adjust to the prevailing conditions suggests that flexibility may be limited in this species.

I also found evidence for differences in behavioural flexibility in zebra finches. In Chapter 4, I found that as individuals gained experience with foraging conditions, their use of the scrounger tactic tended to decline, likely because the payoff for producing increases as individuals become more efficient at exploiting the foraging grid (Beauchamp 2000a; Beauchamp 2006). However, the observed decline in scrounging differed significantly among individuals. Individual differences in the magnitude of behavioural flexibility could occur by random chance if some individuals reduce their use of scrounger more quickly than others, due to chance differences in patch finding rates, for example. Given the frequency-dependent payoffs to producer and scrounger alternatives, other members of the same flock would no longer benefit from reducing their own use of the scrounger tactic, or not benefit as much. In this case, observed individual differences in behavioural flexibility may not be due to differences in the capacity for behavioural flexibility. However, the finding that the extent of behavioural flexibility differed significantly between families (as indicated by comparisons between full-siblings) argues against such differences being the product of random events, and suggests that individuals may show intrinsic differences in their ability to flexibly adjust their use of producer-scrounger alternatives.

Understanding why behavioural plasticity is limited is puzzling, particularly given the obvious advantages to an organism for being able to adjust its behaviour as appropriate for the current conditions (Wolf et al. 2008). Although limited plasticity is often interpreted as being the result of constraints (Sih et al. 2004b), it is not clear why underlying constraints would not be removed by natural selection (Wolf et al. 2008), or why underlying constraints would differ between individuals of the same populations (Dingemanse et al. 2010). Studying consistent differences in an individual's average behaviour and individual differences in behavioural plasticity together may provide new insights into their adaptive nature (Dingemanse et al. 2010).

6.2.3 Group membership decisions

The results of this thesis also suggest that more explicit consideration of group formation decisions in producer-scrounger games may be warranted. To date, models of

producer-scrounger foraging predict the frequency of alternative foraging tactics, given certain parameters such as group size, patch distribution, dominance rank or energy reserves (Barta and Giraldeau 1998; Barta and Giraldeau 2000; Caraco and Giraldeau 1991; Ranta et al. 1998; Ranta et al. 1996; Vickery et al. 1991). None of these models specifically addresses the process of group formation. However, the findings that individuals differ in their use of alternative tactics (Chapters 2, 3, and 4), and that group composition affects the frequency of tactics within the group (Chapter 5), both call into question the validity of ignoring the process of group formation when studying producer-scrounger dynamics.

If individuals are not equally able to use the alternative tactics, the SEF of tactic use may depend on the individuals making up the group (Gross and Repka 1998a; Gross and Repka 1998b). It would be possible to experimentally test this by forming groups of social foragers that differ in terms of the types of individuals making up the group. For example, the SEF of tactic use could be compared between groups of 'producers', groups of 'scroungers' and mixed groups. If the three types of groups differ in their SEF of tactics, it would lend support to the notion that plasticity is limited. If the identity of the individuals making up a group influences the SEF of the group, then the identity of individuals making up the group would also influence the intake rate of group members.

If the SEF of tactic use, and therefore intake rate, depends on the individuals making up a group, then individuals may benefit from being discerning when choosing the individuals with which to form groups. Under the same group size and food distribution conditions, individuals with higher vulnerability to predation, higher basal metabolic rate, or lower body condition have a higher relative use of the scrounger tactic. In order to maximize their foraging intake rate, these individuals should form groups with individuals with a higher propensity to 'produce'.

The preference of individuals with a high propensity to 'produce' is more difficult to predict *a priori*. These individuals would also maximize their foraging intake rate by grouping with other individuals with a high propensity to 'produce', since scroungers reduce the intake of producers (Giraldeau and Caraco 2000; Vickery et al. 1991). However, group

cohesion is greater in groups that contain scroungers (Barta et al. 1997), which may make the anti-predator benefits of grouping greater for groups that contain 'scroungers'. Thus, producers may be predicted to tolerate scroungers in the group as long as the anti-predator benefits they provide in terms of group cohesion are greater than their costs in terms of reduced foraging efficiency (Ranta et al. 1996).

Given the conflicting interests of 'scroungers' and 'producers' in terms of ideal group composition, observed group compositions will depend on who controls group membership. This is analogous to the findings presented in Chapter 5. If we consider group membership at the level of a food patch – the expected number and identity of individuals joining a patch depends on whether individuals are free to choose to join the patch, whether the patch producer excludes individuals, or whether membership at a patch is a compromise between both these processes. A similar process may be at play at the level of the group, with group insiders and group outsiders negotiating group membership. Studies of producer-scrounger foraging in animals that are free to form foraging groups would be useful to understand how the conflicting interests of 'producers' and 'scroungers' with respect to group membership are resolved.

6.3 Conclusion

Social foraging is one of the best-studied systems where individuals use alternative tactics (Giraldeau and Caraco 2000). Although earlier studies have observed consistent individual differences in tactic use (Beauchamp 2000a; Beauchamp 2000b; Beauchamp 2001; Thibaudeau 2004), relatively little is known about the factors that influence individual investment decisions in producer-scrounger alternatives. The results of the research presented in this thesis have yielded several new insights into the factors underlying inter-individual variation in tactic use. In the zebra finch, individuals adjust their investment in producer scrounger alternatives in response to a change in their individual state (such as vulnerability to predation). Furthermore, natural variation in state variables, including metabolic rate and body condition, are related to individual differences in producer-scrounger tactic use. Finally, I developed and tested a model which indicates that individuals may also adjust their

investment in, and tolerance towards, scrounging as a function of their genetic relatedness to group members. Taken together, these findings may have important implications for individual variation in fitness, behavioural flexibility, and group formation decisions.

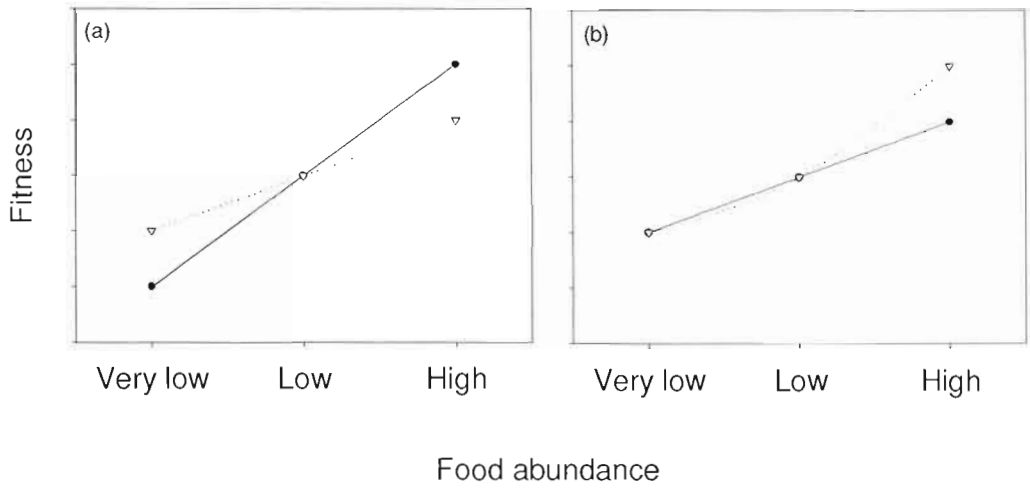

Figure 6.1: Hypothetical phenotype-dependent differences in fitness payoffs under different food conditions. Circles with solid lines represent 'High BMR' individuals; triangles with dotted lines represent 'Low BMR' individuals. In (a), low BMR individuals are less strongly affected by changes in food abundance, resulting in no overall fitness advantage to either phenotype. In (b), both phenotypes perform equally poorly under low food conditions, but 'High BMR' individuals outperform 'Low BMR' under high food conditions, resulting in an overall advantage to 'High BMR' individuals.

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